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NEW BIOLOGY NUMBER 3

New Biology is a miscellany of essays, each an up-to-date account of some aspect of biology which has excited contemporary interest. It is addressed primarily to those who already have a taste for scientific reading. It attempts to present the work of biologists without sacrificing that carefully qualified statement and rigorous argument which scientists use (or try to use) in their technical communications.

Because our contributions are designed mainly for those who already indulge an interest in science, some of them are tough going for readers who know nothing about biology. But other contributions are not difficult, and we strongly urge such readers to try them and see. We have provided for them a glossary of the main scientific terms which are used without definition in the articles.

M. L. J.
October, 1946. M. A.

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HOW A GRASSHOPPER BECOMES A LOCUST

By B. P. Uvarov

THE locust has a claim to be considered one of the oldest enemies of man, and tales of locust plagues go back to Biblical times. There is one curious feature about these plagues, which earned them the name of invasions. For a long period, a country may know no locusts, and then, vast swarms of them appear, and devastate the land for several years in succession, only to disappear again, as if they never existed. For a long time, this periodicity of locust invasions has been one of the major biological puzzles, but the mechanism and the causes of the periodicity have now become better understood.

Locusts are close relatives of the familiar grasshoppers. In fact, it is correct to say that a locust is merely a kind of grasshopper that, at times, occurs in great and dense swarms. Both belong to the insect family of Acrididae, which includes some thousands of species, all vegetarian and all potential enemies of agriculture. Out of that number, less than a hundred different species of grasshoppers are serious pests of crops, but there are only some six to seven species which have earned the name of locusts by their swarming habits.

One of the best studied locusts is the Migratory locust (*Locusta migratoria*) which occurs in many countries of the Old World, including south-eastern Europe. It has been noted long ago that this species is unusually variable in its appearance, and some taxonomists tried to prove that more than one species have been confused under the same name, but recent observations and experiments showed that the variation is closely connected with periodical swarming. It was, in fact, proved that during a swarming period the locust changes its appearance to an extent that may deceive an experienced taxonomist. Similar striking changes were since discovered in other locusts and it is now a recognised fact that all true locusts occur in two *phases*—the solitary and the swarming, or gregarious as it is usually called. The differences between the two phases concern not only the appearance and coloration, but also the physiology and behaviour. The most conspicuous difference between the solitary and the gregarious phase is the coloration of young insects, or hoppers as they are called because they have no wings as yet and move by walking and hopping. Hoppers of the solitary phase are variable in colour, being often uniformly green, but sometimes grey, buff or brown, their colours being always similar to that of their environment. When bred in captivity in differently coloured cages, solitary hoppers develop the coloration harmonising with the background and succulent food induces green coloration. Gregarious hoppers, on the contrary, are characterised by a bold coloration pattern, consisting mainly of black and yellow (or orange) spots and stripes; the pattern is very stable for every species and the coloration does not change in response to the background, or to green food. In the coloration of adults of two phases, the differences are less striking, but they are the same in principle, the gregarious phase being uniform, and the solitary more variable. On the other hand, a gregarious adult undergoes striking colour changes with sexual maturity, when it becomes more or less brilliant yellow, while a solitary adult does not change its colour on maturation.

Even more remarkable than colour differences between phases, are those of structure. In some locusts (*Locusta* *migratoria*) they are so great as to make the two phases look like different insects; in others they can be discovered by biometrical methods. The principal difference is that in the relative length of the forewing and the hind femur. In the solitary phase, the wing is relatively shorter and the femur relatively longer, so that (in *Locusta migratoria*), the ratio forewing/femur is always under two. In the gregarious phase, the wing is relatively longer but the femur shorter, the ratio between them being more than two. This essential phase character holds for other species of locusts, though the actual ratios are not the same. Another phase character is the shape of the pronotum, which in the gregarious phase is short and saddle-shaped, while in the solitary it is longer and decidedly crested; in *Locusta* the two phases differ in that respect to an extent which caused them to be regarded as distinct species. Further differences exist in the head, which in the gregarious phase is relatively wider, and in the size of the eye, which is relatively larger, than in the solitary. Finally, in the solitary phase, the male is much smaller than the female, while in the gregarious both sexes are almost equal in size. The existence of all these characters which can be expressed in measurements and ratios provides an important method for studying phase variation by exact statistical methods.

It is of interest, and obviously of some deep significance, that the two phases in various locust species differ from each other in coloration and structure in a similar way. The underlying principles of phase variation must be, therefore, general. Both coloration and structure being the results of processes of growth, development and metabolism, it is necessary to turn our attention to the comparative physiology of phases. Its study is still very incomplete, but some important facts are already available.

To begin with, the difference in the coloration of hoppers of two phases is a factor of great physiological significance. Insects, unlike warm-blooded animals, have their internal temperature close to that of the surrounding air, but when exposed to direct sunlight they absorb radiant heat at a rate which differs according to their colour. A gregarious hopper which is mainly black absorbs more radiant heat than a green, or buff, solitary hopper, and its internal temperature rises much higher. Direct experiments have shown that, under exactly the same conditions of insolation, a gregarious hopper may develop an internal temperature 5-8° C. higher than a solitary one. Since the rate of all metabolic processes depends on temperature, it is obvious that in a gregarious hopper they will be much faster than in a solitary one, and, possibly, will differ qualitatively as well. It has been established, for example, that the water content of gregarious hoppers is less than of the solitary, while their fat content and concentration of lactic and uric acid in the blood is higher. The rate of respiration is also higher in the gregarious hoppers, even when they are kept completely inactive.

The most significant result of the higher internal temperature of gregarious hoppers is their greater activity. Under the same environmental conditions, a solitary hopper may be inactive when a gregarious one is fully activated; they may, thus, live side by side but, physiologically, in different climates, and the behaviour of a sluggish solitary hopper would differ greatly from that of a gregarious one.

The behaviour of gregarious hoppers in nature is generally characterised by great activity, which attracts the attention even of casual observers because the hoppers live, and move, in more or less large groups, called bands. The typical daily round of a hopper band is as follows. The night is usually spent on plants, where hoppers sit near the tops, densely packed and immobilised by low temperature. When the first rays of the sun strike them, they arrange themselves in such a way as to expose their sides to the sun; their internal temperature rises quickly; they become activated and descend to the ground where they move about, if in the shade, or rest with their bodies perpendicular to the sun's rays, on insolated places; this latter position was aptly named "basking." Further rise in temperature brings about a general movement and the whole band commences marching. The march is an impressive sight, as the band may comprise millions of hoppers, densely crowded and moving relentlessly forward. The march may be interrupted by exceptional heat causing immobilisation of hoppers, but normally it continues all day, and only the falling temperature in the evening slows down the movement, which gradually comes to a standstill. Feeding on plants occurs mainly before the movement starts in the morning, and when it ceases in the evening, but hoppers on the march may also climb plants and eat them up.

While a number of environmental factors may affect the mass movement of hoppers, there is no doubt that the temperature plays the major part as an activator, the radiant heat from the sun being particularly important. This heat, as we know, is absorbed by gregarious hoppers owing to their black colour, and when a hopper marches, its internal temperature rises still higher owing to the muscular exertion. Thus, a marching hopper cannot stop until it becomes sufficiently cool in the evening. In addition, the momentum of its movement is kept up by the continuous stimulation by other hoppers as they jostle each other in their forward surge. Recent exact observations show further that, apart from this mechanical mutual stimulation, the hoppers in a band affect each other even more by the visual stimulation. When a hopper moves forward its neighbour also moves forward, so that the image of the first hopper in the eye of the second remains as it was. This is a reaction that has been called visual compensation, as it results in the movement of an object in relation to the eye being compensated by the movement of the eye (*i.e.*, of the whole insect) in the same direction.

A remarkable feature of band movements is the persistence with which they keep the same direction, unless disturbed. Many ingenious theories have been proposed to account for this persistence, but they all fail to provide a full explanation. The most probable theory and the one best supported by the facts is that the movement is orientated in relation to the sun. We have seen that basking hoppers in the morning are orientated perpendicular to the sun's rays and when they start marching, they preserve this orientation. Naturally, the sun may be either to the left or to the right of a marching hopper, and it appears that the hopper while marching keeps its direction with reference to the sun. That such "sun-compass orientation" exists was proved by ingenious experiments in the field. A marching band, with the sun on the left, was partly shaded and a mirror used to reflect the sun rays so that they fell on hoppers from the right; the hoppers stopped, turned about and marched in the opposite direction, thus bringing the image of the sun back to their left sides. It was found possible to repeat the performance and to make hoppers parade up and down like soldiers.

The most remarkable feature of the mass movement of gregarious hoppers is the fact that the whole band never loses cohesion. Should a hopper jump sideways, it rejoins the band immediately, unless it becomes separated from the band by an obstacle obscuring the view, *e.g.* thick vegetation. There is no doubt that the cohesion of bands is due to the visual interattraction of hoppers. It is not excluded that other senses also play their part, since, for instance, gregarious hoppers of the Migratory locust have a peculiar odour which can be smelt even by a man at a distance of several yards, but exact observations on the olfactory interattraction of hoppers are lacking.

To sum up, the behaviour of gregarious hoppers is characterised, firstly, by a high level of activity. It can be said that gregarious hoppers keep moving unless the temperature or other conditions are such as to make activity impossible. The second typical feature of their behaviour is the interattraction that keeps the bands together.

The behaviour of solitary hoppers is less well known, but its most important difference from the behaviour of gregarious hoppers is the lack of interattraction. If a hopper of the solitary phase is placed in the middle of a marching band of gregarious ones it does not "fall in" and march with them, but makes frantic efforts to jump clear of the crowd. Otherwise, the daily round of behaviour of solitary hoppers is also regulated by temperature, and other weather factors, but the general level of activity is much lower, and they spend more time at rest and on plants than moving on the ground. Persistent marching for hours on end, normal in the case of gregarious bands, is not observed in solitary hoppers. In their behaviour, hoppers of the two phases differ no less than in their appearance, and the difference is biologically much more significant.

Adults of the two phases are also characterised by different behaviour. Again, the most astonishing feature of the behaviour of swarms of the gregarious phase is that a swarm, which sometimes may be not at all dense and which may fly continuously a whole day, still remains a swarm. Some individual locusts may drop out, and settle on the ground for a while, but then they rise again and rejoin the swarm. Exact experiments on the mechanism of inter-attraction of adult locusts in flight are obviously very difficult to make, but observation suggests that the attraction must be visual as in the case of hoppers. It is worth mentioning, however, that night flights are known to occur when the temperature is sufficiently high and it remains a puzzle that a swarm does not disperse in the dark.

Flying activities of swarms are subject to the effects of temperature, as in the case of hoppers, but other weather factors, *e.g.*, wind, appear also important as activators. As a rule, if temperatures are above a certain moderate level, gregarious locusts are more likely to be in flight than at rest. Flying with them may be regarded as a normal state, and rest is enforced by environmental conditions. The factors determining the direction of flight are still imperfectly known, but there is strong evidence that winds above a certain force play an important, perhaps even dominant, part.

The flight may continue for many hours and a swarm may cover literally hundreds of miles before it settles down, though such long flights are, probably, helped by winds. A locust in full flight is in a curious physiological state, since its internal temperature is kept high by the muscular exertion due to wing movements, and it requires a fall in the air temperature, or other sudden weather change, to immobilise the locust and cause it to settle down.

As with hoppers, less is known about the behaviour of solitary adult locusts than of the gregarious ones. One important point is, however, fairly clear, namely that solitary locusts do not take to wing, without being disturbed, as readily as the gregarious ones, and they spend their time mostly at rest. Of course, they do not exhibit the interattraction which is so typical of the gregarious phase.

Such are the characters by which the two phases differ from each other. It must be stressed, however, that these deep and striking differences are found only between the extreme forms, which are connected by a continuous series of transitions. In fact, if the two phases were clearly separated we should have been justified in regarding them as distinct species, whereas they are merely two end links of a chain of individual variations.

Having described the phenomenon of phase variation, we have to turn our attention to the processes involved in the transformation from one phase to another. As the names adopted for the phases show, the characters of one are found in the individuals living singly, while for the other a life in crowds is typical. Experiments with breeding locust hoppers in isolation, or crowded, have proved that the proximity of other individuals, *i.e.*, the density of populations, is the most obvious factor inducing a solitary hopper to become gregarious. When only two or three hoppers of the solitary phase are kept together in a small cage, their colour characters change gradually and they assume the typical pattern of the gregarious phase. Conversely, when a typically gregarious hopper is kept in isolation, it loses its striking colour pattern and becomes indistinguishable from a solitary one. Even in the case of adult locusts, it was found that a typically gregarious individual, when isolated, does not change its colour on sexual maturation, behaving in this respect like a locust of the solitary phase. Such breeding experiments, carried out in cages on a number of species, showed conclusively that phase variation can easily be induced during the individual life of a locust. It was even found possible to make hoppers, by alternating the isolation and crowding, to change their phase more than once during their life-time.

The physiological effect of crowding appears to be in the frequent encounters between individual hoppers, resulting in continuous mutual excitations and leading to intensive activity. Attempts were made to induce higher activity without crowding. An isolated hopper was placed in a long cylindrical cage fixed in a vertical position to an axle; near both ends of the cage there was food and above the upper end there was strong light. Every twenty minutes the cage turned 180°, so that its upper end became the lower and the darker. As locust hoppers have a tendency to climb upwards and are attracted to light, the hopper was made to walk the whole length of the cage every time it turned. As a result, an isolated hopper developed the black pattern and the yellow pigment of the gregarious phase, and it was proved (by repeated experiments) that the development of the gregarious coloration is due to excessive muscular activity, such as would normally occur in a crowd.

In the case of hoppers in the field, a curious physiological situation is created. When hoppers develop black pigment as a result of dense population, they also become more sensitive to the radiant heat from the sun which they absorb more readily and, therefore, are more easily activated. Their greater activity results in further development of black pigment, so that a vicious circle is created: the hopper is active because of its black colour which is due to its high activity rate.

It is, of course, a somewhat simplified explanation of the causes of colour differences between the phases, and until we know more about the biochemistry of locust pigments, we shall not be able to tell why and how the production of black pigment is dependent on the activity.

With regard to the structural differences between the phases, very little research has been done to find out the mechanism of variation. It can only be suggested that the different proportions of parts of the body depend on their unequal rate of relative growth. Thus, the forewings in the solitary hopper appear to grow in length at a relatively slower rate than in the gregarious and a shorter wing results, but we do not know the reason for the unequal rate of growth. In the case of pronotal shape in the Migratory locust a detailed study of the muscles inside the pronotum was made. It is known that insects have no internal skeleton and their muscles are attached to the hard chitinous integument which might be called the external skeleton. As the integument is relatively soft and pliable, particularly just after moults, it is mechanically possible that its shape is affected to some degree by the pull of the muscles attached to it. The muscles that would affect the shape of the pronotum are those that are concerned with the movements of the legs and with the support of the head. A gregarious hopper has to march more than the solitary, therefore its leg muscles must exercise a greater strain on the points of their attachment in the pronotum. A solitary hopper, on the other hand, passes much of its time sitting on plants in a vertical position, when its head needs no muscular support such as is required in a marching hopper. Thus, the change in the pronotum induced by activity can be regarded as an example of the individual response of a growing organism to a modification of behaviour.

While experimental studies in the laboratory have thrown some light on the factors and mechanism of phase variation, it is natural to ask whether the same factors exist in the field and how they work there. It may be argued, for instance, that one can crowd many hoppers in a cage, but how can one expect dense crowding to be achieved in the field where there are no containing walls of a cage? A question of this kind cannot be answered except after careful observations have been carried out, and they served to prove that the theories formed as a result of laboratory work hold good in the field as well. It was thought at first that a population of solitary locusts, living in a suitable habitat, might increase in a year with exceptionally favourable weather conditions so greatly, that the population would become as dense as in an experimental cage. Actually, no such case has ever been observed in nature, and it is difficult to imagine that a population of an area which is not limited can increase to the necessary degree of overcrowding. On the other hand, a number of reliable observations show that the initial concentration of solitary locusts depends mainly on two factors. The first is the sensitiveness of locusts to small changes in temperature and humidity, to which they respond by movements. For instance, in a grassy area of alternating small depressions and hillocks the grass, in a hot and dry summer, will be burnt up by the sun on the hillocks and remain fresh and dense in the depressions. A locust that becomes readily activated by sun rays on bare ground would move about until it gets into a depression where it finds shade and food and will remain there. The same happens to other locusts and they gradually become concentrated in such favoured spots. The second factor contributing to further concentration is that such favoured spots may themselves contract as a result of continued drought, so that the same number of locusts find themselves in a reduced area and, therefore, become more densely crowded. The crowding of this kind may occur either in the case of hoppers, or of adults, but it does not necessarily lead to phase transformation, since even small areas uniformly covered by grass cannot offer the same conditions of crowding as a cage. The actual transformation into the gregarious stage requires still closer proximity, particularly between younger hoppers. This is favoured by the egg-laying habits of female locusts. Eggs are laid by the female in soil, in a cluster of some 30-100 eggs. A female usually selects for laying a bare spot, with suitable soil, which may not be the same in the case of different locusts, but is always of a certain kind for locusts of the same species. If there are few such spots near the concentration area of locusts, whole groups of females will lay their egg-clusters close to each other. Successful development of the eggs depends on a certain degree of temperature and of moisture, and an important point is that all eggs under the same conditions become ready to hatch at the same time. The hoppers, as they hatch, appear on the surface of the soil as a group. Should hatching occur in fairly dense vegetation, hoppers may become separated from each other as soon as they begin to move about. They may also scatter if they hatch on bare ground. When the vegetation is moderately dense, but with some small bare patches, an interesting situation arises. Hoppers which are living as solitary insects amongst the vegetation are activated by the sun and move about on the ground. When, in the morning, the sun becomes powerful, a hopper coming out of the shade on a strongly insolated bare patch assumes a basking position, as has been described above. Other solitary hoppers, happening to come across the same bare patch, behave in the same way and whole groups of basking hoppers are formed. The basking continues until the temperature is reached which activates hoppers, they begin to wander, and the basking groups break up, only to form again towards the evening. If the population of solitary hoppers is fairly dense, and bare patches on which basking takes place are relatively few and small, individual hoppers are bound to come to the same spots and to spend a considerable time every day in close basking groups. The present theory is that, as a result of such fortuitous aggregation, the hoppers become habituated to the proximity of other hoppers and develop the tendency to keep together or, at least, in sight of each other. The habit of gregariousness, is, therefore, an acquired one, and it becomes stronger from the continued association of hoppers in groups. The life in groups inevitably results in a greater rate of activity, owing to mutual excitation, and the black pigmentation characteristic of the gregarious phase makes its appearance. After that, the presence of black pigment will increase the rate of absorption of radiant heat and will lead to intensified activity, resulting in a complete transformation of a solitary hopper into a gregarious one. This process can be slowed down, interrupted, or even reversed, by environmental conditions. If, for instance, good rains cause the vegetation to become dense and tall before hoppers are fully gregarious, their chances of mutual encounter will be reduced, they may revert to inactive solitary life and lose the black pigment. It was observed that a band of fully gregarious hoppers, which happened to march into a large area of dense grass, became disorganised, hoppers lost contact with each other and soon lost the characters of the gregarious phase.

Therefore, the initial aggregation of solitary hoppers depends on the pattern of the environment and the whole process of gregarisation is a matter of interplay between the insect and the environment. Once, however, the hoppers become fully gregarious in habits, their influence on each other overshadows most of the environmental factors, and a band of marching hoppers is much more independent of the external factors than a solitary hopper. When hoppers become adult locusts, the interattraction between individuals is so firmly established that even in flight they tend to keep together. This inevitably leads to the female locusts laying their eggs in close proximity, so that hoppers of the next generation hatching from the eggs soon find themselves in close aggregations. In this way, a solitary grasshopper becomes a swarming locust, a creature of widely different habits.

The reverse transformation, from the gregarious to the solitary phase, can be induced in nature by a number of factors. A swarm may be caused to scatter by a severe storm and eggs will be laid by single females over a wide area; a hopper band may march into dense vegetation and hoppers, losing sight of each other, become less active; eggs in the ground may be decimated by parasites and the few hoppers hatching from them have little chance of aggregation, etc. Again, the transformation depends on an uncertain balance between the environment and the insect.

The scheme of phase transformation in the field as outlined above makes it possible to formulate a general conception of "outbreak areas," that is of the areas where the transformation of solitary into gregarious locusts can occur and the first swarms can be formed. It was thought before that locust outbreaks begin in the areas and in the seasons which are most favourable for the life of the locust, but we know now that this is not the case. In fact, a large population of solitary locusts may live in an extensive and uniformly favourable area without ever having a chance to form concentrations sufficiently dense for phase transformation. It is on the fringes of large favourable areas, where bare, or otherwise unsuitable, patches occur, that conditions for gregarisation are found. There a population of solitary locusts has to lead a somewhat uncertain existence because the extent of the favourable and unfavourable patches tends to fluctuate according to the season and may result in crowding of locusts. This principle can be illustrated by the outbreak areas of the Migratory locust (*Locusta migratoria*), which are found mostly in the deltas of rivers surrounded by semi-desert sandy areas. The solitary locusts live here in grasslands, but the extent and the degree of patchiness of the grass is subject to strong fluctuations depending on the floods, which are irregular since their height depends on the variable rainfall on the upper reaches of the rivers. After a good flood, the area of grassland expands and solitary locusts have abundant food ensuring their multiplication; should this be followed by a very dry season, the favourable conditions will be found only in depressions where locusts would concentrate and become gregarious. The same result may obtain from a set of conditions, which appear to be quite different, in Central Russia. This region is generally too cold and too wet for the Migratory locust which is restricted here to relatively small "islands" of dry sandy soil where overcrowding and gregarisation occurs after exceptionately warm and dry years. Still different conditions lead to outbreaks of the Migratory locust in the Philippine Islands and Borneo. Here the locusts live in grass that grows in areas cleared of the forest in which they could not survive at all. The grass in clearings is subject to seasonal burning by natives, and bare patches result, offering conditions for gregarisation. In the case of the Desert locust (*Schistocerca gregaria*), the outbreak areas are found on the coasts of the Red Sea, where solitary locusts live in small "island" areas in the dry river beds, which are occasionally flooded, so that the extent of habitable areas is subject to sharp fluctuations. Similar instability of conditions is characteristic of the known outbreak areas of all other locusts which have been studied in this respect.

Such is the story of the conditions that make it possible for a harmless grasshopper to become a devastating locust. Apart from the deep scientific interest of the process of phase transformation, the knowledge on this subject which has been accumulated recently is of far-reaching practical importance. In the past, all anti-locust measures could be directed only against swarms of the gregarious phase. However, where an outbreak is allowed to develop, the areas invaded by swarms become so great that it requires a vast and costly organisation merely to defend the crops from destruction. Such purely defensive policy can be justified by the results, but a new knowledge of the origin of outbreaks makes it possible to contemplate a more radical approach to the problem. It is known now that locust swarms do not arise simultaneously over the whole wide regions ultimately invaded by swarms, but originate in the outbreak areas which are relatively few in number and restricted in size. The outbreak areas of several locust species have already been discovered, so that the sources of their outbreaks are known, and it remains now to consider what can be done to *prevent* the formation of the initial swarms in the outbreak areas. The first and obvious step is to ensure that each outbreak area is kept under competent supervision in order to discover any increase in the population of solitary locusts and any tendency on their part to form concentrations. This can be achieved by regular patrolling of the outbreak areas by trained scouts who are able to record the numbers of solitary locusts and to observe whether any concentration and change of the phase characters takes place. As soon as some concentrations of solitary locusts are discovered, steps are taken to destroy them and thus to prevent the initial small swarms from arising.

Such a policy of the prevention of locust outbreaks has been adopted in practice with regard to the Migratory locust (*Locusta migratoria*) and the Red locust (*Nomadacris septemfasciata*) in Africa. In both cases, permanent preventive organisations have been established and the outbreak areas are kept under strict observation and control, with most encouraging results. At the beginning of the year 1945, considerable concentrations of solitary Red locusts were discovered in one of its main outbreak areas; their number increased alarmingly by 1946, and energetic measures were taken to exterminate them, with excellent results. Were this not done, tropical Africa would have been faced with a terrible new invasion which has been successfully prevented.

The outbreak areas of the Desert locust (*Schistocerca gregaria*) which periodically devastates northern Africa, the Middle East and India, are also largely known and plans are afoot to organise their preventive control. No doubt a similar solution will be found to the locust problem in other countries now that the way to it has been found.

Prevention of outbreaks by supervision and timely control measures, however, must continue indefinitely and the vigilance cannot be relaxed without risk of a new outbreak. The present knowledge of conditions of phase transformation makes it possible to hope for an even more radical solution of the locust problem. It is hoped that regular observations and further research into the conditions inducing phase transformation in the field will suggest some means of altering the conditions in the outbreak areas in a way unfavourable for the gregarisation of locusts. The relative extent of grassy and bare patches, for example, may be changed either by drainage or by irrigation, so that solitary locusts will have no chance to concentrate and to transform into gregarious ones. The aim should be to make it impossible for a grasshopper to become a locust. A great deal of patient investigation is required to achieve this aim, but it is not too optimistic to say that the way to the final solution of the locust problem has been made clear by the research on phase variation in locusts.

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FORAGE PLANTS

By D. H. Robinson

IT is not easy to define exactly what is a forage plant, though a good working definition is "any plant whose stems and leaves are consumed by farm livestock." If this description is accepted, it becomes clear that we are dealing with an enormous variety of plants, just as important as those species which are cultivated for their seeds, even though the strict interpretation may rule out such familiar plants as turnips and mangolds, whose edible portion is largely root. Actually it is impossible to classify some cultivated plants as forage plants exclusively, or as grain producers exclusively. Oats, for example, though they are generally looked upon as a grain crop, are frequently cultivated in this country for consumption either as green fodder or as hay. It is a common practice, also, in many parts of these islands to turn cattle or sheep in spring into winter-sown wheat to graze down the plants. This is done either to check the excessive growth of a very forward crop ("Winter-proud," the farmer calls it) which might otherwise lodge or "go down" before harvest: or to provide some valuable grazing for stock, especially dairy cows, at a period when fodder is notoriously scarce. Provided the grazing is completed by the beginning of May little or no harm is done to the wheat, which subsequently grows in a normal way and ripens its grain in the autumn only slightly later than ungrazed corn. Rye is another cereal which is frequently used as a fodder crop. Plants which are usually classed as 'roots' can also be included in a list of forage plants. The sugar beet plant is a 'root' in the eyes of the farmer, yet its leaves, and the crown to which they are attached, form an extremely valuable fodder for many classes of livestock. After the tops (*i.e.*, the crown and the leaves) have been struck off the beet prior to harvesting the roots, they can either be grazed direct on the field by sheep or cattle, or they can be collected and fed to animals in yards, either fresh or as silage. The weight per acre of the tops roughly equals the weight of the roots, and some farmers consider that the tops are as valuable to them as the roots grown for their sugar.

But in talking of forage plants one naturally thinks first of the grasses and leguminous plants which make up the flora of pastures and meadows and one-year leys. The following table sets out the acreages devoted to grain crops and to grassland in England and Wales in 1946, the figures being those set out in the Agricultural Returns of the Ministry of Agriculture.

Acreages of Grassland and Grain Crops, 1946

Temporary grasses and clovers ..	3,712,000 acres
Permanent grassland	9,933,000 „
Grain crops (including beans and peas)	6,863,000 „

The total area in England and Wales devoted to grain and other crops amounts to about 11 million acres; grasses and clovers occupy at least 13 million acres, so it is obvious that these forage plants are of great importance. Yet until quite recently the forage plants of our grasslands were very much neglected. This is particularly true of our native grasses. When Carruthers, in the closing years of last century, was investigating grasses and grassland on behalf of the Royal Agricultural Society of England, he was unable to identify the various species from their vegetative characters, and was compelled to wait until they had flowered before he could name them. Now, certainly the second-year, and often the first-year, student at an agricultural college or farm institute is expected to be able to identify the commoner grass species at any stage of growth. More experienced workers can identify many species merely from the examination of a cross section of a single leaf. This gives some idea of the intensive study which has been made of grassland forage plants during the last 50 years, a study which has had a very great influence upon British farming.

It is a remarkable thing that of the 50 genera of grasses common in these islands, only about five are at all extensively cultivated. More remarkable still, perhaps, that so little was known about any of them until the present century was well advanced. Of course a great deal had been written about grasses in a general sort of way, and the older books on agriculture abound with all sorts of references to the various kinds met with in pastures and meadows. Stillingfleet, about the middle of the 18th century, made some careful observations on grasses, as did William Curtis towards the end of that century. But even 100 years later there was little precise information to be had of the sort that we now take more or less for granted. Sutton and McAlpine, among others, were building up the science towards the end of the 19th century, together with Gilchrist, Somerville, Middleton and Percival. Their work rapidly increased the store of knowledge not only of the individual plants but also of their behaviour in association with each other in grassland. In the early 1920's the establishment of the Welsh Plant Breeding Station at Aberystwyth, with Professor R. G. Stapledon (now Sir R. George Stapledon) as Director, gave a tremendous fillip to grassland work, and encouraged a great number of biologists to take an interest in this class of forage plant.

The grasses upon which most work has been done these last thirty years can easily be enumerated on the fingers of one hand. They are the rye grasses, cocksfoot, timothy and meadow fescue. The clovers thus comprehensively studied are even fewer in number: they are red clover and white clover. Probably the most valuable of all grasses in these islands are the two rye grasses—perennial rye grass (*Lolium perenne*) and Italian rye grass (*L. italicum* or *L. multiflorum*, as it has recently been re-named). Little need be said here about Italian rye grass, which has not been so intensively studied as some of the other useful grasses: it is used chiefly for very short leys intended for grazing or for hay. That is not to depreciate the worth of the grass, which as a short-term fodder plant is almost unbeatable. But since it is short-lived it has not the range of usefulness possessed by the longer-lived perennial rye grass. About perennial rye grass there raged for over half a century a controversy of considerable bitterness. Stapledon[1] has summarised this difference of opinion very neatly. Some agriculturalists praised perennial rye grass very highly as a forage plant, others could not say a good word for the species. The situation became clarified when biologists pointed out that perennial rye grass exists in a great variety of different forms, or strains, some much more leafy, much less stemmy, much later in flowering than others. The sorting out of these different strains has been one of the major contributions of the agricultural biologist during the past 30 years. The work has culminated in the breeding, or hybridisation, of special leafy strains, of which the types known as Aberystwyth S.23 and S.101 perennial rye grass are outstanding examples: the name of Professor T. S. Jenkin, the present Director of the Welsh Plant Breeding Station will always be associated with this valuable plant. This grass, S.23, has been accused of being relatively unpalatable to livestock, and in the dry, eastern parts of the country it has not been universally accepted as superior to "commercial" strains. But over the rest of the country S.23 rye grass has had an influence upon pasture formation which is scarcely less than sensational. Its extreme leafiness and capacity for forming numerous side shoots are extraordinary. Cocksfoot, too, has undergone extreme modification at the hands of Stapledon and other hybridists. The older works on farming speak rather disparagingly of the plant as "rough" cocksfoot, and refer to its coarseness and tufted habit of growth. These disadvantages have been very largely overcome by selectors and breeders, and there are now available strains which are smoother to the touch, with a very much higher proportion of leaf to stem. There has been, as in the case of perennial rye grass, a great sorting out of types of cocksfoot. Distinctive strains come from New Zealand and Denmark, and from Aberystwyth the hybrids S.37, S.26 and S.143, designed respectively for the purpose of hay, hay-with-grazing, and grazing. Timothy has received similar attention, and farmers can now obtain a number of different strains varying from the stemmy American types to the ultra-dwarf, specially leafy Aberystwyth S.50.

Of the clovers, it is convenient to deal first with red clover *Trifolium pratense*). Until the late R. D. Williams published his findings about 1923, there was great confusion in the minds of agriculturalists and agricultural botanists concerning red clovers. In simple but masterly language Williams showed that there are three main classes of red clovers:—wild red, early-flowering red, and late-flowering red clovers. He was able to relate all the known types of red clover grown for fodder into one or other of these classes, and he did much to banish from seed catalogues such time-honoured but misleading descriptions of red clovers as "giant hybrid cow grass," and "colossal double-cut cow grass." As a result of the investigations of Williams and others, the farmer is now well provided with information about the suitability of certain types and strains of red clover to special needs and conditions—information which must have added greatly to the productivity of grasslands.

The history of white clover is one of the romances of agriculture. Sixty years ago the virtues of wild white clover were practically unknown to farmers in this or any other country; yet to-day it is recognised as one of the most valuable forage plants in existence, around whose peculiarities is built up almost the whole of our present-day system of grassland farming. White clover, of course, differs essentially from red and alsike clovers in having a prostrate stem, which runs along the surface of the ground and roots vigorously at the nodes. The edible portions are the long-stalked leaves and flower heads. Until about 1886 the white clover in common use was the Dutch white type, a large-leafed but short-lived plant, which soon died out from newly sown grassland. Then the attention of botanists was drawn to the fact that there exists in good old grassland another, wild, form of white clover which, though smaller in the leaf and therefore less productive than Dutch white clover, is truly permanent. Twenty years passed, and then it was discovered that the comparatively new phosphatic fertiliser called basic slag had a remarkably stimulating effect upon the growth and vigour of wild white clover. Both on poor, heavy clay in Northumberland and on poor, chalky soil in Sussex, basic slag was found to have a miraculous effect upon pasture land. For the slag encouraged the clover, which in turn passed some of its nitrogen on to the grasses: the increased quantity of fodder thus produced permitted a larger head of livestock to be maintained, whose dung still further enriched the land. Similar spectacular results were obtained on most of the soil formations throughout the country, and it became apparent that wild white clover is a plant of great value. The original experiments showed that wild white clover can be stimulated whenever it occurs naturally in grassland: subsequent investigations demonstrated that the plant can readily be introduced into farm land by sowing the seed as a constituent of seeds mixtures. Almost unknown to farmers and sold by a small number of seedsmen at 1/6 per lb. in 1907, the price rocketed to 35/- per lb. in 1920 when the vast areas of land being sown down to grass after the 1914-18 war created a huge demand for the seed. Fortunes were made by a small number of farmers in Kent who specialised in the harvesting of Kentish wild white clover from old grassland. From that time on to just before the outbreak of the last war, wild white clover reigned supreme among leguminous forage plants in the formation of new grassland. But now its position, so far as leys of up to four or five years' duration are concerned, is threatened by yet another form of white clover. It is a type which is very much more vigorous in growth than the true wild white clover, with thicker stems and larger leaves, yet which is longer lived than the Dutch white clover. There are two representatives of this class of white clover: one is the type native to certain pastures in New Zealand and known as New Zealand "Mother" white clover; the other is a hybrid developed by the late R. D. Williams and known as Aberystwyth S.100. The two are very similar, and because of the ready way in which they establish themselves from seed and rapidly cover the ground, and because of the quantity of fodder they produce, they have greatly simplified the formation of leys. It has been repeatedly demonstrated during the last 20 years that the success or failure of a newly sown ley depends very much upon how quickly white clover will establish itself; if it covers the ground rapidly, thus keeping out weeds, knitting the grasses together and stimulating them with their nodule-collected nitrogen, the ley is likely to succeed right from the start. A poor establishment of white clover, on the other hand, greatly handicaps a ley, and this is one of the main reasons why our grandfathers, who did not understand the use of this clover, had such extreme difficulty in laying down land to good grass. It is not easy for us to-day to understand what an anxious and expensive operation it was even as recently as 50 years ago to attempt the formation of a good pasture, though the agricultural journals of the time are full of references to the subject. The use of wild white clover and S.100 white clover, together with an understanding of these plants' reaction to phosphatic fertilisers, has greatly simplified the task of grassland establishment. In many districts, too, the interaction of S.100 white clover and Aberystwyth S.23 perennial rye grass has led to a completely new technique for producing medium duration leys. The conventional seeds mixture for 3-4 year leys usually contains about 30-35 lb. of mixed grass and clover seed per acre, and this mixture is customarily broadcast and harrowed in after the 'nurse' crop of barley or oats or spring wheat has been drilled. During the last five years, however, ultra-simple seeds mixtures have been very successfully used in various parts of the country, notably Buckinghamshire, the prescription per acre being on the following lines: 6 lb. S.23 perennial rye grass; 3-4 lb. S.100 or N.2 mother white clover. The total seeding, in other words, is only 10 lb. per acre. These seeds are mixed with the barley and sown simultaneously with it, through the ordinary corn drill; frequently the fertiliser is also sown simultaneously if a "combine" drill is available. The extraordinary tillering or shoot-producing properties both of the rye grass and the white clover lead to the formation of a productive sward within a few months of the removal of the cereal crop. It is essential that the specified strains of rye grass and clover be used, for only these have, so far, the power of rapid turf formation from such a low rate of seeding.

A leguminous forage plant which needs special mention is Lucerne, or alfalfa (*Medicago sativa*). Lucerne is possibly the oldest forage plant in cultivation, and its other name, alfalfa, is derived from a Persian word meaning "the best fodder." It is characterised by a very lengthy, penetrating tap root, and by a capacity for producing cut after cut of green leaves and stem when once properly established. The fodder is very rich in nitrogen, and very palatable both when green and when made into hay. The plant has been grown in these islands for a very long time, and those who read old books on agriculture cannot fail to notice how often during the last 200 years lucerne has been hailed as the salvation of British farming. Yet, despite its advantages, lucerne has never become truly popular here. Its drought resistance, its productivity, its excellent feeding value, its deeply penetrating roots—all these qualities have been recognised and publicised for generations by those who have grown it successfully. Perhaps the reason for its comparative neglect lies in the concluding words of the previous paragraph, for lucerne is not always easy to establish from seed. One of the reasons is that most soils in this country lack the special bacteria capable of forming the root nodules essential to healthy growth of the plant. In common with all leguminous plants, lucerne can grow really successfully only if there is the symbiotic relationship between the lateral roots and the nitrogen-fixing bacteria—a relationship whose most obvious evidence is the presence of characteristic wart-like root nodules✓ Plants growing in a soil deficient in the requisite organism do not develop the nodules, and their growth is stunted. Although inoculation of deficient soils has been practised over the past half century or more by sprinkling infected soil over the land, or over the seed before planting, it is only very recently that it has been demonstrated that some strains of the lucerne nodule organism are much more efficient than others. During the last 25 years the most vigorous strains have been selected out, and have been made available in cultures for the use of farmers wishing to grow lucerne. The use of these cultures has to some extent simplified the establishment of lucerne, but it has not led to the extension of the area under the crop which at one time seemed likely. It is now being realised that we know very little about the different strains of lucerne whose seed is imported into these islands: failures with lucerne may be due to the use of strains which are unsuited to local conditions. For example, the so-called "Grimm" lucerne of North America can be of very mixed origin. Some Grimm types originate in almost tropical conditions, while others come from districts having extremely cold winters. Attention is therefore being directed towards separating these various strains and testing them out in various parts of this country. When this has been done over a series of years the prospective grower should be much more favourably placed than hitherto.

It is now being suggested, as the result of recent trials, that lucerne needs a "companion" grass if it is to be really successful, in much the same way as grasses need a "companion" clover. The reason may not be the same in both cases, but the practical result may be. So far, the most widely used companion grass for lucerne has been cocksfoot, but experience has shown that cocksfoot is too aggressive, and tends to smother out the lucerne in two or three seasons, though for a year or two the yield of fodder from such a combination may be extremely satisfactory. Meadow fescue seems to fit into the picture rather more neatly, and timothy also is promising.

We are learning, also, that lucerne is no mean grazing plant if managed in the right way. In this country there has been a tendency to regard the plant almost solely as a provider of green fodder to be cut either for hay, for silage, or for feeding green. But the great success which has attended the local use of lucerne-with-cocksfoot grazing leys in East Anglia has made agriculturalists realise how little they know about the grazing potentialities of lucerne, and is certain to lead to extended experiments in the near future.

There is great need in this country for really successful, *annual*, leguminous forage plants. Leguminous plants are needed because of their ability to collect nitrogen cheaply from the air, for nitrogen is expensive to buy, both as manure and as a food. Unfortunately for the farmer, most of our leguminous forage plants take more than one season to develop properly. There are exceptions, like beans, peas and vetches, but these are far from being ideal as fodder. The clovers all take more than one year to develop, with the exception of crimson clover, or Trifolium (*Trifolium incarnatum*) which is too hairy and stemmy to be of general use. It must be remembered that the so-called one-year ley is really a season and a half old before it is utilised as hay, for the seeds are sown in a cereal crop the year before the fodder is sown. A fodder crop of the leguminous type which can be sown and used within the space of, say, five months would be welcomed by farmers, but sad to say no satisfactory alternative to our existing annual legumes, peas, beans and vetches and trifolium, seems yet to be available. Attempts have been made repeatedly to develop annual leguminous species, but so far without much success. Among the most interesting plants experimented with are lupins, soya beans and "sweet clover."

Annual lupins are of three kinds, white, yellow and blue. Certain types are familiar in gardens, having been developed particularly for their flowers. Cultivated lupins are similar in general appearance to these garden types. The white variety is a giant type not generally used for fodder, but both the yellow and the blue lupins have been used here for feeding sheep since about the middle of last century. Lupins are capable of growing in soils which are so acid, or deficient in lime, that most crop plants fail to develop. For this reason they have been used quite successfully on thin, sour sands in Suffolk, Nottinghamshire and elsewhere. If not folded off by sheep the plants are ploughed in to enrich the soil with humus and nitrogen. Many farmers on this class of land, however, fight shy of lupins because of "lupin-poisoning", brought about by a poisonous alkaloid called lupino-toxine: they fear to fold sheep on lupins because of the risk of losing, in particular, pregnant ewes, and cattle cannot be pastured upon the crop. During the last 10-12 years workers in Germany have been able to select out from the ordinary bitter lupins types of non-poisonous, "sweet," lupins in which the toxic alkaloids are absent. There are both yellow and blue sweet lupins, and preliminary experiments carried out in Suffolk by Oldershaw[2] have shown that both the herbage and the seed can be safely fed to sheep, cattle, pigs and poultry. It is yet too early to forecast the future of sweet lupins as a forage crop, but on light, poor land they may prove to be a useful addition to the farmer's list of home-grown, high-protein fodders.

The soya bean plant has been grown for probably 5,000 years.[3] It is one of the oldest of farm plants, and was first described in an ancient Chinese work on *materia medica* of 2838 B.C. It is very extensively cultivated in the countries of its origin, China, Korea and Japan, and since 1910 has developed into a very important crop in the United States of America. Its seeds are manufactured into an astonishing variety of substances varying from food stuffs to linoleum and printing ink. The growing plant can be pastured, cut green for "soiling" to livestock, or made into hay. The remarkable growth in popularity of soya beans as a source of fodder in U.S.A. naturally led to experiments in this country to find out if the plant could repeat its performance over here. These experiments must not be confused with those designed to determine the possibility of growing soya beans for their seed. These seed-growing attempts received a great deal of publicity some years ago when carried out on a large scale on an estate in Essex, but little real success was achieved. A dry season enabled a useful weight of seed to be harvested on one occasion, but the success was not repeated, and we still lack a strain of soya bean which can be relied upon to ripen its seeds in this country. It is remarkable that more intensive efforts have not been made to investigate the soya bean as a supplementary fodder crop in these islands, certainly in the warmer, drier regions. Some small scale experiments were made at the Harper Adams Agricultural College in Shropshire from 1925 to 1928, when it was estimated that the varieties under test gave about 7 tons per acre of green fodder. Since, according to Borst and Thatcher, the percentage of crude protein in the dry matter of the soya bean plant may be as high as 22 per cent, the weight of protein per acre represented by a growing crop is considerable. It is not easy to understand why the forage possibilities of a plant which has proved so successful in the United States have not been more closely investigated. Granted that initial experiments may have been unsatisfactory, the prize to be won is so valuable that continued efforts should be well worth while. There is tremendous variation in the types of soya bean grown both for grain and for fodder throughout the world, and one of the first tasks is obviously to sift out the likely ones from the impossible ones by growing the various strains in comparable conditions in this country.

American sweet clover, or Bokhara clover, is really a melilot (*Melilotus alba*). The plant, which has a romantic history, is a native of these islands, resembling lucerne in its vegetative parts. It was introduced into North America about 1739, probably as an impurity in farm seeds, and it established itself so well and developed so rapidly that it became a troublesome weed, particularly in young stands of lucerne. The plant is characterised by an extremely long and penetrating root, and by a stem at first succulent but rapidly becoming tough and woody. It occurred to workers in America that this strong-growing weed might be made use of as a fodder plant. When it became clear that the stem is palatable and digestible until it is about a foot high, and that the successful utilisation of the herbage depends primarily on accepting its habit of turning into wood almost overnight, melilot rapidly became popular as an additional forage plant. Now it is regularly planted on thousands of acres of land every year in Canada and parts of the United States, and is used for pasturage and for cutting green. White melilot is a perennial plant, but an annual type has been developed under the name Hubam. This is a composite name, derived partly from that of Professor H. D. Hughes of Iowa Agricultural Experiment Station, who in 1916 discovered some melilot plants which flowered in their first year; and partly from the Alabama seed, sown in Dakota, which also gave rise to some annual types. In these islands "sweet clover" has not yet achieved much recognition, though the plant can undoubtedly be grown successfully on those very poor gravelly and chalky soils which most benefit from a thorough penetration by long, inquisitive tap-roots like those of melilot. One of the reasons for its neglect, no doubt, is the rapid change from palatability to indigestibility exhibited by the stem. Yet Friend Sykes[4] maintains that, from his own experience, no legume grown in England can compare with sweet clover in the nitrogen fertility that is left behind. He uses the plant both as a fodder crop and as a humus and nitrogen-producing plant for ploughing in. He states that a properly managed crop of sweet clover will, in its second year, give four or five cuts for silage, each cut being made when the plant is 8-9 inches high. For "sheet composting" Sykes recommends grazing the first growth, then cutting the subsequent growths when they reach a foot in height and allowing the herbage to lie and rot. The whole mass of semi-decayed material is then ploughed under during October.

It is not sufficient merely to grow grasses and clovers—the fodder must be utilised to the best advantage, and this means not only that pastures must be properly grazed, but also that much of the fodder must be preserved for winter use. The age-old method of drying fodder into hay is still with us, and is likely to remain an essential feature of agriculture as long as farming is practised. Modern science has not advanced the practice of making hay to any startling extent, though it has emphasised by chemical analyses what practical farmers have known for a very long time, namely that grass cut at or before flowering makes better quality hay than grass which has been allowed to go far beyond the flowering stage into the period of seed formation. Some of the first reliable analyses of hay were made by Voelcker getting on for 100 years ago, and they showed that certain species of grasses and clovers are more nutritious at the hay stage than others. Voelcker's figures were more or less confirmed by other chemists, but the astonishing thing is that no one anywhere in the world took the trouble to analyse grasses and clovers during the early stages of growth. Not until the 1920s did Woodman, of Cambridge, analyse grass only a few inches tall: and when he did so he experienced a tremendous shock. He discovered that young, succulent grass is vastly different from grass at the hay stage. It is a concentrated food stuff very rich in protein, so rich, indeed, that it can be compared with linseed cake. Later the fact was established that such grass is also very rich in carotene, the precursor of vitamin A.

These discoveries not only explained many points concerning the grazing of livestock, but also opened up a vast field of speculation and experiment. Would it be possible, for example, to preserve this young, concentrated forage in a palatable form for winter use? The problem of preservation was tackled from two angles, those of grass drying and of silage making. After a great deal of preliminary investigation, in which agricultural chemists and engineers worked in close co-operation, a reasonably satisfactory grass-drying machine was put on the market about 1936. During the last decade (despite the stumbling block of the war) a number of different types of drier have been developed, and grass drying on a big scale is now by no means an uncommon farm operation. The problem is to convey the young, freshly-cut grass to the drier; evaporate the water rapidly without scorching the grass or destroying the carotene: and store the dried product in a convenient manner. The actual evaporation of water is now achieved by exposing the grass to currents of warm air in trays, in revolving drums, or on continuous conveyors : the dried product is either compressed into bales fastened with wire or string, or is ground to a fine powder in a hammer mill and bagged in paper containers. Because of the present shortage of imported concentrates, this ground-up grass meal finds a ready sale, at prices determined by its carotene content: as a rule, the carotene varies between 200 and 350 milligrams per kilo. The apparatus necessary for drying grass is costly to instal, and quite a lot of labour is required for cutting and handling the material. The process, though it is likely to expand very considerably when materials for erecting the drying plants are more plentiful, cannot become in any sense universal.

But the other method of fodder preservation, through ensilage, requires no expensive apparatus, yet provides a good quality, palatable, winter food for stock. Early attempts to preserve very young grass in silos were not altogether satisfactory, for the fodder frequently took on a bad colour, went sour and soggy, or rotted into waste. Eventually it was discovered that the real cause of these disappointments lay in the protein-rich nature of the young grass. Ensilage, of course, has been practised for a very long time, but the material filled into the hollow towers, or silos, has usually been green stuff in a much more mature condition, such as oats and vetches cut just about flowering time, or maize at about the same stage of development. Such fodder, especially when chopped up before being blown into the silo, is soon acted upon by bacteria which feed upon the carbohydrates of the plants, giving rise to lactic acid. This, and similar organic acids, preserves the silage from decay, so long as air is prevented from entering the mass. Young green grass, however, is so rich in protein, and relatively so deficient in carbohydrate material, that the lactic organisms are unable to feed themselves and produce the essential lactic acid. This difficulty has now been overcome by adding a soluble carbohydrate to the green material as it is being filled into the silo. The usual practice is to sprinkle, through a watering can, about a gallon of molasses on every ton of green fodder. The silage is encouraged to heat up spontaneously to a temperature of about 90-100° F, and is finally sealed off and weighted down by a layer of soil. There is a move towards pit silos on many farms : a pit silo is merely a trench dug in the ground to convenient dimensions and, if properly drained, the wastage in these pits is less than that commonly experienced in many tower silos made of wood or concrete. Silage made from young grass contains much more protein, calculated on a dry matter basis, than average hay, which is a bulky carbohydrate fodder. Good grass silage may have up to 20 per cent protein in the dry matter, whereas much hay has only 5-10 per cent protein.

During the last few years the making of kale silage has become popular in various parts of the country. Two kinds of kale are widely grown as fodder crops in this country, namely thousand-head kale and marrow-stem kale. Thousand-head, or open-head, kale has been known for a very long time, and its hardiness has made it a favourite amongst Brassica crops for the feeding of sheep and cattle in districts subject to frosts in winter. But since the beginning of the century its place has largely been taken by the newer plant, marrow-stem kale, introduced here from France. This plant has a very thick stem full of pith, as well as a large spread of leaves, and it is relatively rich in protein—in fact, as a protein producer for livestock it ranks very high amongst green fodder plants. But marrow stem kale becomes increasingly coarse and fibrous after Christmas and it is not so hardy as thousand-head kale. To prevent wastage many farmers now turn their kale into silage well before Christmas. The plants have to be chopped up before being put into the silo, but no molasses are needed because there is enough soluble carbohydrate material in the plant to permit the preliminary bacterial action. Kale silage keeps very well if properly made, and closely resembles the original plants in chemical composition.

The growing of herbage plants for seed has never been a major department of British agriculture—in the past we have been, as in so many other things, content to import the bulk of our requirements. But there has always been a small forage seed growing industry, situated principally in the drier eastern and south-eastern parts of the country. The harvesting of seed of "evergreen" types of perennial rye grass, of wild white clover, and of crested dog's tail has long been a subsidiary industry in parts of Kent. Devon and Cornwall have also shared in the harvesting of perennial rye grass, in these counties designated "eaver." Red clovers of distinctive types have long been saved for seed in Suffolk, Hampshire, Montgomeryshire, the Vale of Clwyd and elsewhere. Wild white clover seed is harvested in very many counties, under a scheme administered jointly by the Ministry of Agriculture and the National Farmers' Union: in 1945 some 2,586 acres of old grassland were inspected under the certification scheme.

The development of the Aberystwyth strains of forage plants has swelled the ranks of the seed growers. These strains were only in their infancy immediately prior to the war, and their seed was being grown on a quite small scale by enterprising farmers in Herefordshire and elsewhere. During the war the cutting off of supplies of foreign seed gave a great impetus to the growing of the "S" strains, and some idea of the rate of development can be obtained from the table below.[5]

Development of Aberystwyth Strains

		Acres Harvested			
		1941	1943	1944	1945
S.23	Perennial rye grass ..	533	1,812	3,538	4,360
S.101	Perennial rye grass ..	92	389	722	1,698
S.37	Cocksfoot	53	258	803	1,376
S.26	Cocksfoot	226	557	1,090	1,968
S.143	Cocksfoot	172	401	772	1,733
S.48	Timothy	7	53	325	710
S.51	Timothy	10	85	74	202
S.100	White Clover	242	1,123	3,691	4,891
S.184	Wild White Clover ..	—	—	259	789
S.123	Red Clover	162	760	1,120	891
S.151	Red Clover	—	98	370	481
		1,497	5,536	12,764	19,099

In the multiplication of these strains great care is taken to maintain as closely as possible the standards originally set by the breeders of the various plants. These Aberystwyth strains are amongst the very few fodder plants having a standard of excellence which is recognised by seedsmen and farmers alike, for none can be sold as genuine unless the growing crops have been inspected and "certified." Each year, at the beginning of May, a number of trained agricultural biologists meet at the Welsh Plant Breeding Station to refresh their minds concerning the finer points of inspection technique, and then disperse throughout the country to inspect the crops. The inspection, certainly of the rye-grass crops, has to be carried through in a matter of a fortnight or so, and the inspector's reports are then considered by the station staff who decide whether or not to issue a certificate in respect of each crop.

Some of the seed is disposed of through wholesale agents acting for Seed Growers' Associations, while in other cases the larger seed firms contract with the growers to take the crop at an agreed price. The retail price of the "S" strains is determined annually after consultation with the various bodies concerned—grower, wholesaler, retailer and consumer. This price has, so far, been considerably higher per lb. than that of the commercial grades of the same species of plant. For example, for 1947 the retail price of S.23 perennial rye grass is 3/6 per lb., while "commercial" types of perennial rye grass have been purchasable at 1/- per lb. upwards. This enhanced price is due partly to a realisation on the part of farmers that the "S" strains are superior in many ways to existing commercial strains and that they are of a guaranteed standard: and partly to the extra cost of growing the seed. The leafy grasses and clovers naturally produce fewer seed heads than the stemmy types—that is why they are so valuable as forage plants—and consequently they produce a less weight of seed per acre. Also the care needed in growing, inspecting and handling has to be paid for. Home growing of forage plants for seed has been a sheltered industry since the outbreak of war, and farmers are aware that they will have to become increasingly efficient at the job if they are to continue to grow seeds at prices competitive with those of overseas growers.

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THE MENACE OF THE ROUNDWORM

By Geoffrey Lapage

ON the first page of the Report on Sheep Diseases compiled by the Survey Committee of the National Veterinary Medical Association of Great Britain and Ireland the disturbing statement is made that a conservative estimate of the mortality inflicted by the ten major diseases of sheep is £1,009,600 a year. First upon the list of these diseases given in this report is the form of inflammation of the stomach and intestines which is caused by various species of the kind of animals which are called roundworms. The biologist calls them nematodes, because he must distinguish them from other and quite different kinds of animals to which the name "worm" is also given. The inflammation of the alimentary tract of sheep (and of that of other farm animals also) which is caused by parasitic roundworms is called by the veterinarian parasitic gastro-enteritis. Some veterinarians call it verminous gastro-enteritis, because it is caused by parasitic "worms." The report just mentioned tells us that the annual cost of the mortality of sheep caused in this country by this disease alone amounts to £348,000, which is about a third of the total annual cost of the mortality caused by the ten major diseases of sheep. It should be noted that this is an estimate of the cost of the actual deaths of sheep only. If we include the depreciation of the market value of sheep which do not die from the effects of roundworms but fail to thrive well because of their effects, the farmer's financial losses will reach a much higher figure. In the United

States, where the numbers of sheep reared are very much greater, the annual loss has been estimated to amount to hundreds of thousands of dollars a year. The farmers of the Dominions and of other countries also rear far greater numbers of sheep than the British farmer does, so that their losses also are proportionately greater than they are in this country. When we reflect that parasitic roundworms cause a similar disease of cattle as well as of sheep, the full significance of the losses inflicted by these parasitic animals can be realised. All countries rely for their supplies of meat and milk upon the rearing of healthy sheep and cattle. Other countries, moreover, import British stock for breeding purposes and the vigour and health of British breeding stock is deservedly famous and must be maintained. In addition to this, some species of parasitic roundworms—species which are different from those which cause parasitic gastro-enteritis of sheep—are the causes of other diseases of sheep, cattle, pigs, poultry, ducks, geese and other domesticated livestock.

Roundworms parasitic in farm animals are, therefore, among the most powerful of the enemies of man, for they menace his food supplies, upon which his very existence depends. Nor is this the whole story of their menace. There are species of roundworms which are parasitic in plants and some of these severely damage essential crops, such as wheat, potato and beet. Yet other species of them are parasitic in man himself. Among these latter are the hookworm, parasitic in his alimentary canal, and the filarial worms, parasitic in his lymphatic and other tissues, both of which bring misery, illness and death to countless human beings, especially in the warmer countries of the world. The thread or pin worm is another species of roundworm which annoys man. The Guinea worm, which is probably the species to which the name "fiery serpent" is given by the Bible, is a roundworm which attacks man in the tropics. It is clear, therefore, that we have ample reason for attacking the roundworms by every means that we can devise. But we shall not succeed in our war upon them unless we base our attack upon a detailed knowledge of their life histories and biology. It is one of the aims of this article to show how important it is that we should have this knowledge and how important it is that it should be as detailed and accurate as possible.

In the first place, what is a roundworm like? Most of the species of roundworms are relatively small. The biggest species known is *Dioctophyme renale*, which lives in the kidney of the dog, the mink and some other animals. Occasionally it has been found in the kidney of man. It is sometimes called "the scarlet scourge" and may attain a length of about a yard and the thickness of a little finger. That is, however, a gigantic size for a roundworm. Many of the species of roundworms which are not parasitic and which live in the soil or in water are hardly or not at all visible to the naked eye and are therefore little known to anyone but microscopists and biologists. Some of the species which are parasitic upon plants are also very small, while the species parasitic in animals and man are usually bigger and can be seen by the naked eye.

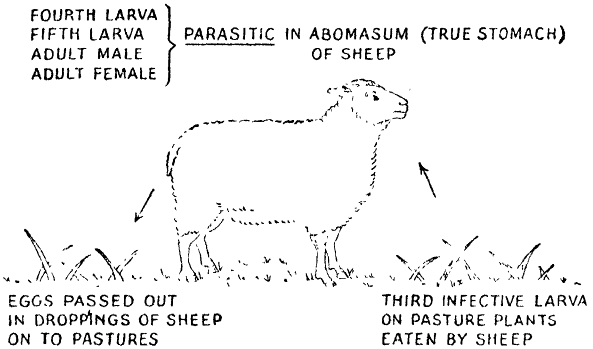
A typical roundworm is cylindrical in shape, its body being pointed at both ends and not divided, as the body of an earthworm is, into a series of segments whose existence is indicated by a series of rings upon the surface of the body. The surface of the body of a roundworm appears to the naked eye to be smooth and glistening. The outer covering of the body (cuticle) of some species is transparent, so that many of the details of the internal structure can be seen through it. This is especially a feature of the small non-parasitic species. Some of the larger species, however, have a thick and opaque outer covering, which gives them, when they are alive, a creamy-white appearance something like that of polished, wet porcelain. Some peculiar features of the structure of roundworms, those, for instance, of the muscles and the cuticle, are not found in any other kind of animal. The sexes of roundworms are always in separate individuals and the males are fewer and smaller than the females. We know very little about the physiology of roundworms and more knowledge of it is urgently required. It is evident, however, that roundworms have been very successful forms of life, because the number of the species of them is very great. Some experts, indeed, think that we shall eventually learn that there are more species of roundworms than there are of insects.

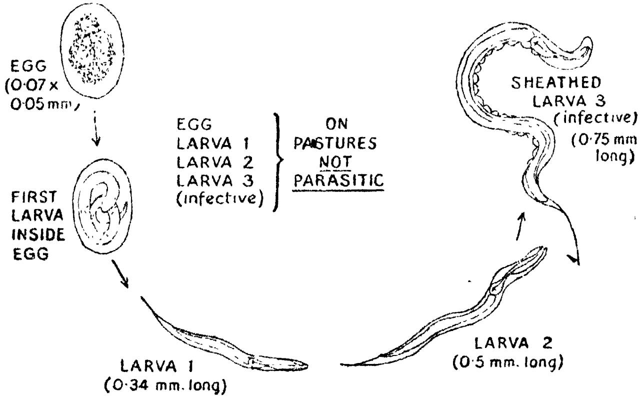
Although their structure is remarkably uniform, the roundworms can live in almost any kind of situation in the world. Species which are not parasitic have been found, for example, in deserts, in the sea and in fresh water, in soil, sewage and in vinegar barrels; and roundworms were recovered by the Shackleton expedition from Antarctic ice. The numbers of these non-parasitic species present in particular localities may be very large. Thus it has been estimated that the soil of some regions examined contained three thousand millions of roundworms per acre and that the upper 20 millimetres of beach sand examined contained 1,500 millions of them. The individuals of some species parasitic in some plants may also be very numerous. It has been estimated that there may be some 11,000 to 90,000 specimens in a single gall formed upon wheat as the result of the activities of the parasitic species *Anguillulina* (*Tylenchus*) *tritici*. Very large numbers of some of the species parasitic in animals may also be present. When, for example, sheep are heavily parasitized by the species which live in their intestines, 50,000 individuals belonging to various species may be present and the fourth stomach of a single sheep has yielded enough individuals of the species *Haemonchus contortus* to fill a pound jam jar. Usually, however, the numbers of roundworms present are fewer than this, especially when the host animal is healthy. The numbers present vary according to the species of roundworm, the resistance of the host animal to them and other factors, some of which are discussed in the course of this article. Whatever their numbers, however, roundworms may attack practically any tissue of the animal body. As a basis for our study of the particular problem with which this article is concerned, namely, the control of roundworms which are parasitic in the alimentary canal of the sheep, let us first consider the life history of one species of roundworm which is a common cause of inflammation of the true stomach or *abomasum* of sheep. This is the last of the four chambers through which the food of all ruminant animals must pass after these animals have chewed the cud; from the abomasum the food passes directly into the first part of the intestine which is called the *duodenum*.

The species which we are to consider is *Haemonchus contortus*. This species is sometimes called the barber's pole worm, because, when it is alive, its long, white ovaries can be seen coiling round its intestine, which has a reddish colour imparted to it by the blood which it has sucked from the abomasum of the sheep. It is sometimes also called the large stomach worm. The female *Haemonchus contortus* is about ¾ to 1¼ inches long and about one-fifth of an inch thick. The male of the same species is only about ½ to ¾ of an inch long and about one-sixth of an inch thick. The males can be recognised by the presence at their hinder ends of an umbrella-like expansion of the outer covering (cuticle), which is supported by rays of a stiffer material. This is the copulatory bursa which aids the male to adhere to the female during copulation. The possession of a copulatory bursa places *Haemonchus contortus* in the Order Strongyloidea of the Class Nematoda, because only members of this order possess this structure. Its shape and the arrangement of the rays which support it are used, together with other features of the structure, to establish the various genera and species of Strongyloidea.

The female *Haemonchus contortus* lays in the abomasum some 5,000 to 10,000 eggs per day and these eggs pass down the alimentary canal and out with the sheep's droppings. The egg of this species is similar to that which is produced by many other species of Strongyloidea. It is oval and transparent, with a clear, clean outline. It measures about 0.07 by 0.05 mm. and, by the time that it has been passed out of the host, its contents have usually divided to form 16 to 32 cells. From this egg, when the external conditions are suitable, emerges a first larva. The shape of this larva is very like that of its parents. It feeds upon the bacteria in the droppings in which it is hatched and grows until it moults its skin. It is then called the second larva and this also feeds upon bacteria and moults its skin. The second larva, however, does not cast off its skin as the first larva does. This skin remains upon the third larva into which the second larva has grown. This third larva, therefore, is enclosed in this cast skin of the second larva and cannot feed. It must exist upon the food granules which are stored up in its intestinal cells and it cannot develop further until it is eaten by another sheep. If this does not happen it dies when its food stores are used up, provided that it is not killed, as countless numbers of these sheathed, third larvae are, by the environmental factors to which they are exposed. When it is eaten by a sheep, this sheathed third larva breaks its way out of the sheath which encloses it and becomes parasitic in the abomasum of sheep. The sheathed third larva is therefore the phase of the life history which infests new hosts and for this reason it is called the *infective larva.* Neither the first nor the second larvae can infest new hosts. If either of them is eaten by a sheep, it is destroyed by the sheep's digestive juices. It takes at least three days for the infective larva to develop from the egg.

The infective larva of *Haemonchus contortus*, and that also of other species commonly parasitic in the alimentary canal of sheep, gets into the sheep by way of the mouth and only by this route. When it is mature it climbs up the leaves of the pasture plants and is eaten with these by the sheep. In the mouth of the sheep it emerges from its sheath, this emergence being helped by the chewing action of the sheep's teeth and also by the physical effects upon the sheath of the alkali in the sheep's saliva. Released from its sheath, the third larva passes down into the abomasum of the sheep and there develops under the mucus on the walls of this organ. The presence of large numbers of these roundworms provokes a copious secretion of mucus by which the roundworms and their larvae are protected. In the abomasum the larvae shed their skins twice. The third larva, that is to say, moults its skin and becomes the fourth larva and the fourth larva moults and becomes the fifth larva, which then develops directly into the adult. The fourth and fifth larvae, however, cause abrasions of the walls of the abomasum and live underneath the blood clots which are formed over these. The adult males and females which develop from the fifth larvae pass all their lives in the abomasum. They pierce the walls of this organ and suck blood from it. *Haemonchus contortus* therefore causes, in addition to the irritation and inflammation which result from the activities of its larval and adult phases, considerable loss of blood. If many of these roundworms are present, a severe anaemia may develop. Among the signs of this anaemia are pallor of the membranes which line the sockets of the eyes and of the mucous membranes which cover the gums of the teeth. The sheep becomes listless; it loses appetite and weight; it may develop a swelling under the jaws which is called "bottle-


FOURTH LARVA
FIFTH LARVA
ADULT MALE
ADULT FEMALE
PARASITIC IN ABOMASUM (TRUE STOMACH) OF SHEEP
EGGS PASSED OUT IN DROPPINGS OF SHEEP ON TO PASTURES
THIRD INFECTIVE LARVA ON PASTURE PLANTS EATEN BY SHEEP



jaw." Diarrhœa may or may not be a symptom of infestations by *Haemonchus contortus*, but this species may cause emaciation and even healthy animals may die quickly if the infestation is heavy enough.

The life history of *Haemonchus contortus* is thus a simple life cycle which can be represented by Figure 1. It involves two very different modes of life, namely the non-parasitic life of the egg and the first, second and sheathed third larvae and the parasitic life of the later larval phases and of the adults. Infestation of the host is only by way of the mouth, a method of infestation which is called the contaminative method; and it can be effected only by the third larva. It is therefore obviously important that we should study carefully this third infective larva and learn as much as possible about its mode of life and its relationships to its surroundings and the methods by which it may get into the mouth of the sheep; for, if we can kill it or prevent its entry into the sheep, we shall prevent the disease which the adult phases cause. This study of the mode of life of any animal and of its relationships to its surroundings and to other animals is called the study of the *bionomics* of the animal.

The application of our knowledge of the bionomics of the non-parasitic larval phases of *Haemonchus contortus* is described below. Here we may note that some species of parasitic roundworms are not confined to entry into their hosts by way of the mouth. This is the commonest of all the methods by which parasitic animals enter into their hosts, but some species of them can use other portals of entry. These other methods of entry are described in the writer's Pelican book *Parasitic Animals** and in the other books recommended for further reading at the end of this article. One of the most important of them is entry by penetration of the outer covering of the host, because the power of doing this increases enormously the parasitic animal's chances of entry into a suitable host. The infective larvae of the hookworms which infest man possess this power of skin-penetration and normally enter man through his skin, although they have retained the power of entering him through the mouth. One of the species parasitic in sheep, *Strongyloides papillosus*, also produces skin-penetrating larvae. This power of skin-penetration makes it more difficult to prevent the infestation of the hosts by species whose larvae possess it and it is fortunate that most of the species of nematodes which infest farm stock can enter their hosts only by way of the mouth. A brief note on some of the other species which may be present in the alimentary canal of the sheep will help us to understand the importance of the study of them.

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* Now in preparation.

It is a curious fact—and one which has not been explained—that the various species which are parasitic in the alimentary canals of ruminant animals each inhabit definite regions of this canal. In the abomasum of sheep, for example, we find, in addition to *Haemonchus contortus*, species of two other genera, which are very much smaller. These are species of the genus *Ostertagia*, an example of which is *O. circumcincta*, a slender, brownish species, about half an inch long, which is usually found to be most numerous near the entrance of the abomasum into the next part of the alimentary canal, the duodenum, and may cause a severe gastritis; and *Trichostrongylus axei*, a very small species about a quarter to a third of an inch long. In the duodenum, which immediately succeeds the abomasum, we find other species of the genus *Trichostrongylus*, all of which are very small. They are all very injurious, partly because they damage a part of the alimentary canal which digests and absorbs the food and therefore controls the nutrition of the host. Species of

Trichostrongylus often cause a blackish-green diarrhœa, which is called "black scour" by some farmers; and also anaemia, weakness and loss of condition similar to that which is caused by *Haemonchus contortus*, In the duodenum we may also find *Strongyloides papillosus*, the adult females of which burrow into the walls of the duodenum and cause inflammation and consequent diarrhœa. Lower down the small intestine we may find species of the genus *Cooperia*, which are about two-fifths of an inch long; species of the genus *Nematodirus*, which reach a length of half an inch; and the blood-sucking hookworm, *Bunostomum trigonocephalum*, which may be an inch long and is stouter and therefore more easily recognised. In the colon of sheep, which is part of the large intestine, there may be the species *Oesophagostomum columbianum*, which is about three-quarters of an inch long. Its larvae burrow into the walls of the colon and develop there for periods varying from about five days in young sheep to three to five months in older ones. These larvae cause the formation in the walls of the colon of nodules which have given rise to the name *nodular worm*, which is given to this species, and to the name *pimply gut*, which is applied to intestines damaged by it. The effects of this species may be very serious. In Australia it is regarded by some experts as being the most dangerous of all the roundworms which are parasitic in the alimentary canal of sheep. Other species of *Oesophagostomum* attack cattle and pigs. Heavy infestations of sheep with this species may kill them quickly and lighter ones, especially if they continue, cause diarrhoea and anaemia and all the consequences of these afflictions. Badly-infested animals develop a peculiar stiff, awkward gait, with a humped back; and paralysis of the hind-quarters may precede death. Another species found in the colon is *Chabertia ovina*, a stout, creamy-white species about three-quarters of an inch long, which is sometimes called the large-mouthed bowel worm. This species, if it is present in sufficient numbers, can cause weakness, emaciation, diarrhoea and anaemia. In another part of the large intestine, namely the caecum (blind-gut), we may find the whipworm *Trichuris ovis*, which is easily distinguished by the fact that the anterior two-thirds of the body of the male or the anterior four-fifths of the body of the female is thinner than the posterior part, so that the whole nematode has the appearance of a whip with a short handle. This thin anterior part of the nematode is buried in the wall of the caecum and the nematode feeds by sucking in the tissue fluids of the host. Its effects are not, however, usually so serious as are those of species of the genera *Haemonchus*, *Trichostrongylus*, *Ostertagia*, *Bunostomum* and *Oesophagostomum*.

While all these species and also some others may be found in British sheep, it must not be supposed that all of them will be found in any and every individual sheep, or even in every sheep which is suffering from disease caused by parasitic roundworms. Some of them are more injurious than others and the species most likely to cause this kind of disease in British sheep are *Haemonchus contortus* and the species of *Ostertagia* and *Trichostrongylus*. Species of *Oesophostomum* and *Bunostomum* may also be found in British sheep and, if they are present in sufficient numbers, they have serious effects. Because some species are more injurious than others, it is necessary, when we suspect that ill-health of sheep is being caused by parasitic roundworms, to find out what species are present in the sheep and also to estimate the relative numbers of the different species present. Examination of the eggs passed in the droppings will not give us an accurate estimate of the relative numbers of the species present, nor will it help us much to find out what these species are, because the eggs of most of them are so much alike that they cannot be distinguished by their microscopic appearances. The only species found commonly in the alimentary canals of British sheep whose eggs can be readily distinguished are species of the genera *Nematodirus*, *Strongyloides* and *Trichuris*. The parasitologist must therefore examine directly the contents of the alimentary canal of the sheep. If a sheep dies as a result of the infestation he can examine the contents of the alimentary canal of this sheep; if none die, it may be wise to slaughter one or more in order to make a more precise diagnosis. The results of the examination of the alimentary canal of any one sheep will, however, apply only to that particular animal and it will not follow that all the sheep of the same flock contain the same species of parasitic roundworms or even the same relative numbers of the species found. It is for this reason wiser to examine more than one sheep if this is possible.

Examination of the contents of the alimentary canal is done by a dilution method of which the following is a brief outline. The different parts of the alimentary canal are examined separately, but it is not usually necessary to examine more than the first half of the small intestine, because the most injurious of the species of roundworms which live in this organ will be found in its first half and many of them in its first few feet. The contents of each part of the alimentary canal are washed out with water or dilute formalin into capacious jars or other receptacles. It is important that the walls of the part of the alimentary canal under examination should be searched for any roundworms which may still be adhering to them and these are added to the contents washed out. The whole of the material thus obtained is then made up with water or dilute formalin to a known quantity of fluid—say 4 litres (4,000 cc.). Successive samples of this fluid are then passed through a coarse wire screen to remove the larger débris. Some parasitologists prefer to omit this screening, in case it may remove some of the larger roundworms. The material is then vigorously stirred and, while it is being stirred, a sample of 40 cc. is removed and the number of roundworms present in this sample is counted by pouring it in small successive amounts into a glass dish placed over a black background, which shows up the roundworms and makes it easier to see them. The number of roundworms in the sample of 40 cc. gives, when it is multiplied by 100, the total number of roundworms present in the part of the alimentary canal being examined. The total number present in the rest of the alimentary canal can be obtained in a similar way.

Provided with this knowledge of the approximate numbers of roundworms present in the whole of the alimentary canal or in the different parts of it, the experienced parasitologist can usually form an idea whether there are sufficient numbers of them to cause disease. He will, of course, take into consideration the fact that some species of them are more injurious than others; he will also consider the presence or absence of other diseases and other factors which may be affecting the health of the particular sheep which he is examining. Broadly speaking it can be said that, if the symptoms shown by the sheep suggest that they are suffering from the effects of roundworms, and, if the abomasum contains more than 15,000 roundworms of all species, these roundworms are probably causing disease. In general it can also be said that, if the intestine contains more than 15,000 roundworms of all the species which inhabit this part of the alimentary canal, it can be concluded that the roundworms are causing disease. Total counts of 50,000 to 100,000 may, however be obtained from heavily-infected sheep. When more than one species is present, or when sheep are debilitated by any other cause, smaller numbers than those just given may cause disease and most parasitologists would agree that experience alone can enable the observer to form a reliable opinion about the effects of the roundworms present in any particular flock. The figures which have been given should, therefore, be taken merely as a rough guide and can never be the sole basis for a diagnosis. They refer, moreover, to sheep only. The relative numbers of the species of roundworms which may cause disease of the alimentary canals of cattle, horses and other animals are different.

Another method of getting an idea of the degree of the infestation of animals with roundworms is the method of counting the approximate number of roundworm eggs in the droppings of the animals. This method, which is also applied to infestations of man with hookworms, is useful provided that the many fallacies to which it is subject are taken into account. Some of the methods of counting the eggs are based upon the dilution principle, the eggs being counted in a small sample of 0.1 cc. or so of a suspension of a known quantity of faeces in a known quantity of either water or of a solution of sodium hydroxide. Other egg-counting methods use the principle of flotation. They employ a fluid which has a high specific gravity, such as a saturated solution of common salt or of zinc sulphate. In these solutions the eggs float to the surface, from which they can be recovered. A flotation method which is much used nowadays is the one devised at the McMaster Laboratory of the University of Sydney. It is called the Gordon-Whitlock method, these being the names of the two workers who devised it. The method requires a specially constructed slide, which provides two, or sometimes three, chambers, the capacity of which is known, which can be filled with a suspension of 2 grammes of the animal's droppings in a saturated solution of common salt. In this solution the eggs float up to the under surface of the glass top of the chamber, through which they can be counted under a low power of the microscope. Within a few minutes, by this method the parasitologist can determine the number of eggs present in 1 gramme of faeces and from this figure he can form an idea of the degree of the infestation present. He cannot, however, determine by this method the species which are present, because, as we have already explained, the eggs of the most injurious species are so much alike that they cannot be distinguished microscopically. It will usually be necessary to do egg counts on more than one sample of faeces because the number of eggs per gramme passed out in the droppings may vary enormously from day to day or even at different times on the same day; and several other factors have to be taken into account in the interpretation of the egg count. If, however, sheep are passing out more than 2,000 eggs per gramme of faeces, it will usually mean that they require treatment for infestation with nematodes present in the alimentary canal. If the animals are cattle or horses, fewer eggs per gramme than this will usually indicate the presence of numbers of adult roundworms sufficient to cause disease.

The Control of Disease caused by Roundworms parasitic in the Alimentary Canal.

The species of roundworms which are parasitic in the alimentary canal can be attacked by two methods. First, we can try to kill their adult and later larval phases while these are in the alimentary canal of the host. To do this we administer to the host chemical substances which will, we hope, kill the roundworms. These substances belong to the group of drugs which are called *anthelmintics* (or *antihelminthics*), a name which is derived from the term *helminthes*, which is given by biologists to the roundworms, tapeworms and flukes. Second, we can try to prevent the host from being infested by the roundworms. To do this effectively we must know all that we can about the method by which the host is infested and about the characteristics and mode of life of the infective larva and also those of the eggs and larval phases which precede it. These two methods of attack are usually combined and the relative importance of each will depend upon whether we are trying to combat a condition of disease from which the sheep are already suffering or are trying to prevent the occurrence of this disease in a flock of healthy sheep. It is important, therefore, to consider first what we mean when we say that roundworms present in the alimentary canal of sheep are causing a state of disease.

The condition which we call disease is not necessarily produced by the mere entry of a parasitic organism into the body of the host. All animals harbour many different kinds of parasitic animals, but the healthy host of them establishes a state of equilibrium between itself and the parasitic organisms and this equilibrium enables both the host and the parasitic animals to live. This state of equilibrium depends upon several factors, among which are the numbers of the parasitic organisms present, their relative virulence, the state of health and constitution of the host, and the resistance (immunity) which the host develops both to the effects of the parasitic organism and also to the increase within the host's body of the numbers of the parasitic organism. Important also is the past experience which the host has had of the parasitic organism, for any kind of parasitic organism will, as a rule, cause more severe effects in a species of host (unusual host) which has not been accustomed to its presence than it will in a species of host (usual host) in which the parasitic organism has been parasitic for many generations. The age of the host also exercises considerable influence; usually the young animal will suffer more severely than the older one. All these, and other factors also, must be taken into consideration when we are studying the equilibrium established between any particular host and the organisms parasitic in it. As a general rule, however, we can say that parasitic organisms cause disease only when some factor intervenes to disturb this equilibrium. If, for example, the general health of the host suffers as the result of poor feeding or exposure to climatic effects such as cold and wet, the host cannot maintain its equilibrium and its resistance to the parasitic organism may be overcome. The parasitic organism then increases its numbers or its effects and causes a degree of injury of the host which we call disease.

It is evident, therefore, that, whatever the virulence of the parasitic organisms may be and whatever influence other factors may be exerting, a certain minimum number of individuals of the parasitic species must establish themselves in the body of the host before a state of disease can arise. Every individual infective phase of the parasitic organism does not succeed in establishing itself inside the host. Normally, in fact, countless numbers of them fail to do this, so that mere exposure to infection is not sufficient to bring about a state of disease, or even the risk of it. We have, moreover, to distinguish between two different ways in which the numbers of parasitic organisms may be increased inside the host. Some kinds of parasitic organisms, such as the bacteria, and the single-celled animals which are called Protozoa, an example of which is the malarial parasite of man, are able to multiply inside the bodies of their hosts. If, therefore, only one individual infective phase of these species enters a host and finds in it conditions favourable to its development, this single infective intruder may multiply and may quickly produce so many descendants that the host is unable to cope with their combined effects. A state of disease of the host then arises in a relatively short time. Other species of parasitic organisms, on the other hand, cannot multiply inside their hosts. To this group the parasitic roundworms belong. Each infective phase of a parasitic roundworm can give rise to one adult phase only. It follows, therefore, that the number of roundworms present in the host can be increased only by the entry into that host of more and more individual infective phases. Because disease cannot arise until a certain minimum number of infective phases have succeeded in establishing themselves and in developing to the adult state, diseases caused by parasitic roundworms develop relatively slowly. *Haemonchus contortus*, for example, requires a minimum of about three weeks to develop from the infective phase to the adult state; large numbers of its infective larvae normally fail to enter the sheep and many of those that do enter will fail to develop to maturity in the sheep's alimentary canal. In resistant sheep, especially, large numbers of them are destroyed, because the effect of this resistance is that the early parasitic larval phases are either killed or fail to reach maturity. Resistant sheep, to put it in another and in perhaps a clearer way, tolerate in their alimentary canals only a certain number of parasitic roundworms; the presence of these in them produces in the sheep a resistance which enables the sheep to destroy large numbers of the infective larvae subsequently taken in; so long as the rate of intake of these additional infective larvae is not overwhelming, the resistant sheep will not acquire a heavy infestation and is not likely to suffer from disease caused by the parasitic roundworm. If, however, its resistance is broken down by poor feeding, exposure to severe climatic effects, the debility caused by other diseases, or other factors, even the most highly resistant sheep will run the risk of suffering from parasitic gastro-enteritis.

We are now in a better position to understand the real problem which confronts the sheep farmer. It is not so much a problem of preventing altogether the entry into his sheep of the infective larvae of parasitic roundworms. This, it may be said at once, is an impossible task under normal farming conditions. It is difficult enough, even when all the resources of a modern laboratory are available, to rear, for experimental purposes, lambs which are free from roundworms. To attempt to do this on the farm would be ridiculous. The farmer's problem is rather to prevent the parasitic roundworms which are inevitably present in his sheep from increasing their numbers to such an extent that a state of disease is produced in the sheep. It is with this object that he applies the two methods of control which have been mentioned above. Let us consider these two methods in turn.

Treatment of the Sheep with Drugs.

Any attempt to remove the roundworms from the alimentary canals of sheep can be only temporarily beneficial. The adaptations of the roundworms to the habits of their hosts are so efficient that, under normal conditions, re-infection of the sheep is sooner or later inevitable. All our plans must, therefore, assume that re-infestation will occur. Next we have to realise that even the best of known anthelmintics will not infallibly remove all the roundworms from the sheep. Roundworms are killed with great difficulty and, although a great deal of research has been done, especially during recent years, with the object of finding a cheap, reliable and effective anthelmintic which will kill roundworms, we have yet to find a chemical substance whose action can be regarded as being satisfactory. Most of the anthelmintics now in use are very poisonous to the hosts of the roundworms and all of them must be regarded as dangerous drugs. They should be administered only by persons who are well acquainted with the dangers associated with their use. The anthelmintics most often used in this country for the purpose of killing roundworms parasitic in sheep are phenothiazine and a mixture of copper sulphate and nicotine. In other countries other substances are also used, among which is tetrachlorethylene. For the treatment of roundworm infestations of other animals the choice of the anthelmintic will be different and we cannot discuss this complex question further here. An adequate discussion of it would involve the consideration of the varying toxicities of the various anthelmintics to different species of host animals and would occupy the rest of this article. We must content ourselves with saying that treatment of sheep with anthelmintic substances designed to kill the roundworms parasitic in their alimentary canals is valuable when flocks have acquired infestations which threaten to cause disease, or even when the sheep are actually suffering from disease. It is also valuable to administer anthelmintics periodically, say, two or three times a year, in order to reduce the numbers of roundworms present in a flock, so that there is the less danger of the increase of the numbers of these to a level which will cause disease. If, however, the number of sheep is large, or if they are grazing over very wide areas of hill or prairie land, the cost and labour of rounding them up for this periodical "worming" may be so great that it is not an economical proposition. The farmer has to balance the total cost of producing his sheep against the total profit they will bring to him, and he may have to give priority to economic rather than to biological and veterinary considerations.

The Prevention of Infestation.

The methods by which the farmer may attempt to reduce the degree of infestation of his sheep with roundworms parasitic in their alimentary canals depend upon the studies which biologists have made of the life histories of these species of roundworms and of the modes of life of their non-parasitic and infective larvae. We have learnt that the eggs of *Haemonchus contortus* are deposited upon the pastures, that the first and second and third larvae to which the eggs give rise are not parasitic, that the third larvae alone can infect the sheep, and that this third larva can infect the sheep only through its mouth. We have also learnt that this third, infective larva crawls up the vegetation of the pasture and is eaten by the sheep when it crops the pastures. We have also learnt the important fact that each infective larva can give rise to only one adult roundworm, so that the degree of the infestation of each sheep will depend upon the number of individual infective larvae which it takes in. Our tasks, therefore, are first to do everything that we can to prevent the development of these infective larvae and second, to limit as far as possible the number of them which the sheep can take in. An idea of the numbers of them with which we have to contend can be gained from the work of E. L. Taylor, who is parasitologist to the Ministry of Agricultural Veterinary Laboratory at Weybridge. Taylor has recorded that an average sheep pasture which he examined carried some 200 infective larvae per pound of herbage, while a pasture which had been grazed by a flock of sheep suffering from parasitic gastro-enteritis carried between one and two thousand of them per pound of herbage. How can we attack these prodigious numbers of infective larvae and how can we attack the eggs and earlier larval phases which precede them ?

We cannot kill the eggs or larvae by applying chemical substances to the pastures, because the only substances which we know which will kill the eggs and larvae will also kill the pasture plants. Nor would it be possible to apply such substances to the very large areas grazed by sheep in the Dominions and in the United States, or even to the larger British grazing areas. It would be difficult to apply them even to small areas in concentrations sufficient to kill appreciable numbers of the eggs and infective larvae. We can, however, destroy some of the eggs and larvae by careful disposal of the droppings of the host animals. Usually it will not be possible to apply this method to the droppings of sheep, but it can be applied to these when sheep are kept on small areas of land or to the droppings of other animals which are kept on restricted areas. The hand collection of manure is, for example, a useful means of controlling the infestation of valuable racehorses with the roundworms (redworms) which infest their alimentary canals, because these animals are kept either on small paddocks or in "boxes." Some benefit may also result from the stocking of manure in manure heaps. The heat and fermentation in these heaps will destroy many of the eggs and infective larvae and some of the substances present in urine may also do this. For the same reason the use of silage for feeding will do something to prevent roundworm infestations, because the infective larvae will be less likely to survive in silage than in hay. It is not, however, likely that heavy infestations can be acquired from hay under normal conditions, although infective larvae derived from hay, especially if it is damp and insufficiently matured, can theoretically be the starting point of infestations which may later cause trouble, especially in animals which are debilitated or are for any other reason feebly resistant to the roundworms.

Another method by which we can destroy some of the larvae on the pastures is to take advantage of the fact that some species of roundworms are able to live only in some species of hosts. The species of roundworms which live in the alimentary canals of sheep cannot, for example, live in the alimentary canal of the horse and its relatives; nor can those species which live in the alimentary canal of the horse live in the alimentary tract of sheep. If, therefore, we graze horses on a pasture infected with the infective larvae of roundworms parasitic in the alimentary tract of sheep, the horses will ingest these larvae and they will be destroyed by the digestive juices of the horse, in which they cannot survive. For the same reason horses can be protected from the infective larvae of the species of roundworms which infest their alimentary canals by putting sheep to graze upon the horse paddocks, so that they can take in and destroy the infective larvae of these species (redworms). E. L. Taylor has, in fact, estimated that, when a flock of sheep was placed on a horse paddock which carried some 6,000 infective redworm larvae per pound of herbage, *each member* of the flock of sheep could take in and destroy some 60,000 to 90,000 infective redworm larvae. It is not wise to use cattle in this way for the removal of the infective larvae of species which infest sheep, because many of these latter also infest cattle. We can, however, use sheep themselves for this purpose, provided that they are sheep which are, or have been, already infested and have developed the resistance to further infestation which has been mentioned above. These will usually be older sheep and we can reserve uninfected ground for the young lambs, which are not resistant. We have already explained that when animals develop a resistance to roundworm infestation of this kind, one effect of it is that only a certain number of the roundworms are able to maintain themselves in the resistant sheep and that the infective larvae which are taken in after this resistance has developed either fail to develop to maturity or are killed. These resistant sheep will, therefore, destroy many infective larvae on an infected pasture. Care must be taken, however, that poor feeding or any other cause does not break down their resistance to the roundworms.

It is, of course, always necessary to guard the young lambs as much as possible from infestations, because the young animal always suffers more severely than the older animal does. This age resistance, as it is sometimes called, is characteristic of resistance to diseases caused by several different kinds of organisms which cause disease and it should be distinguished from the kind of resistance which develops as a result of an infestation. The factors upon which it is based are not yet fully understood and cannot be discussed here. It is important to note, however, that if resistant ewes are grazed with their lambs in the manner just suggested, there is a serious danger of infestation of the young lambs. Some systems of sheep management, indeed, graze the ewes and the weaned lambs upon separate pastures and reserve any available uninfected pasture for the lambs. This is a feature of some types of the progressional grazing which is mentioned below.

Another method of preventing heavy infestations with roundworm infective larvae is the use of what are called "bare lots," which are areas of land on which there is no grass, so that the infective larvae must remain upon this bare ground, on which the conditions for their development are not so favourable as they are upon the pastures. The idea underlying the use of these bare lots is that fewer infective larvae will develop on them and, because the sheep are not eating grass up which the larvae normally climb, they cannot pick up so easily any infective larvae that do develop. It is doubtful, however, whether these are correct assumptions, because sheep penned in houses or yards with concrete floors readily acquire heavy infestations from the larvae which develop in their own droppings; and it is well known that it is dangerous to pen sheep upon arable land, into which the sheep trample their droppings, so that a medium is formed which is very favourable to the development of the infective larvae.

Whatever method of management is adopted, however, it is important to avoid putting too many animals upon any particular piece of land. The number of sheep per acre must be carefully estimated, because overstocking leads to heavier contamination of the ground. The value of wide areas of grazing land is well shown by the fact that, in the United States, in areas where pastures are very extensive, the sheep may be entirely free from such species as *Haemonchus contortus* or may be only lightly infested by roundworms. When, however, the same sheep are brought into smaller areas of pasture, they become more heavily infested. It is for this reason that farmers who have only relatively small grazing areas have developed the practice of moving sheep at intervals of time from one piece of land to another. This practice is a very valuable means of controlling roundworm infestations and is called *rotational grazing*. When sheep are moved in this way at short intervals of one to three days, the practice is often called "folding". We have learnt earlier in this article that a minimum of about three days must elapse before the larvæ which hatch from the eggs of the roundworms which we are considering can develop to the infective phase which alone can infect the sheep. In cold, dry weather a longer time will usually be required; and individual larvæ will require different periods of time for their development. If, therefore, we pen sheep on small plots of land and move them to a fresh, uncontaminated plot every day, or even every three to five days, we shall be moving them before the infective larvæ derived from their own droppings can have developed and we shall reduce appreciably the number of these larvæ which they can take in. Many of the older shepherds knew this by experience and, long before the biological reason for it was known, this practice of moving sheep on from plot to plot was often used. It is probably the basis of the saying, which has been attributed to Yorkshire shepherds: "Never let the lambs hear the church bells twice from the same piece of land". This saying, however, interesting as it is, implies that the sheep are moved only once a week, which is too long an interval. In East Anglia many farmers move them every day and land which has been used in this way for folding is kept free from sheep for at least a year. This policy has been very well rewarded by comparative freedom from disease caused by roundworms.

The practice of folding or rotational grazing is, of course, impossible unless sufficient land is available. It also involves much fencing and management and therefore increases labour costs. It can hardly be applied to the very large flocks of thousands of sheep which are reared in the Dominions and the United States. Nor is it so necessary to apply it to these flocks, which can roam over relatively enormous areas of land. It is a method most suitable to the small farmer. It should not be confused with *pro-*

gressional grazing, which is the practice of dividing a farm into three or more areas, two of which are used each year for grazing, one being allocated to the lambs, while the third is either left as pasture free from sheep, or is grazed by animals which cannot be infested by roundworms parasitic in sheep, or is ploughed in and resown with grass, or is used for a year for growing some other crop. This third area is thus given a rest from grazing which lasts a year or longer. During this time most of the infective larvæ upon it will be destroyed by climatic conditions. Some of them will also be destroyed by ploughing, which buries them ; but it must not be assumed that ploughing will destroy all of them, because it has been shown that the infective larvæ of some species of parasitic roundworms can regain the surface of the soil after they have been ploughed in. The most efficient system of all will be a combination of progressional grazing with rotational grazing, which not only separates the ewes from the weaned lambs, but institutes on the grazing areas a system of rotational grazing which prevents the animals from grazing any particular area of land for longer than a day or two.

The fact, mentioned above, that the infective larvæ climb up the foliage of pasture plants and are then eaten by the grazing animal, has important bearings upon the prevention of roundworm infestations. The infective larva also moves away from intense light and from darkness. Further, it requires a moist environment and is relatively quickly killed by drying. More infective larvæ will therefore be found upon the pasture plants at dawn and dusk, when the light is dim and the dew is still on these plants, or when similar conditions prevail during the daytime after rain or when the skies are overcast. For these reasons the practice of bringing in grazing animals for the night is a good one, although it can only be applied to small numbers of them.

The movements of the infective larvæ are, however, influenced also by the structure of the pasture plants. E. L. Taylor has studied this question and has shown that the collar which clasps the stem of some species of grass at the junction of the leaf and the sheath can deflect infective roundworm larvæ along the under sides of the lower leaves, so that sheep, which tend to select the more succulent upper leaves, avoid the larvæ on these lower leaves. Clover, on the other hand, offers no such obstruction to the progress of the larvæ, so that heavier infestations may be acquired from this plant. The application, moreover, of some fertilisers, such as basic slag, which encourage the growth of clover. may for this reason encourage also the acquisition of roundworm infestations. The infective larvæ, which develop in the droppings upon the ground, will, moreover, find it more difficult to ascend plants, such as sainfoin, which make a relatively less extensive contact with the soil. E. L. Taylor, in fact, found that samples of sainfoin carried 550 larvæ per pound, while grasses examined under the same conditions carried 1,900 larvæ.

The grazing habits of the animals themselves also influence the degree of the infestations which they pick up, but we have not space to discuss these here. It will be evident, however, that animals grazing upon tall pasture plants will usually acquire lighter infestations than animals which graze upon short grass. They will also get more nourishment from the taller, more vigorous plants and will therefore be in a better condition to resist such infestations as they may acquire. For this reason some farmers have encouraged the rapid growth of new grass by the application of nitrogenous fertilisers and have grazed animals upon this, hoping in this way to reduce the degree of the infestation with nematodes and also to improve the nutrition of their lambs. One advantage of this practice is that the lambs graze for shorter periods and so reduce the time during which they can take up infective larvæ. Heavy infestations can nevertheless be acquired under this system and they may be masked by the improved nutritional condition of the animals. The animals may, that is to say, be so fit and resistant that they do not show symptoms of disease, but they may at the same time be harbouring relatively large numbers of roundworms and may therefore heavily contaminate pastures and be the source of infestation of other stock. When, on the other hand, animals graze on short grass or on grass of poor quality, or even on recently sown grass between the individual plants of which there is relatively more exposed earth, they will get less nourishment from these pastures and will be less resistant to the roundworms; they will also tend to tear up the pasture plants together with the roots and soil in which the roundworm larvæ are sheltering. Heavy infestations are likely to result from both these causes and they are most likely to be acquired in winter, or at times of drought, when the growth and quality of pasture plants is poor. Drying will kill many of the larvæ, but many will survive even long periods of natural drought. If a wet spell interrupts the drought, these survivors will become active, so that heavy infestations may follow these wet spells.

The resistance of the infective larvæ to drying and to other climatic conditions is nevertheless remarkable. They can remain alive even after they have been dried to a degree which renders them unrecognisable as roundworm larvæ and they can be blown about in the air, just as bacteria are. Their powers of resistance to heat, cold and other climatic factors have been studied experimentally and we know that the infective larvæ of some species are more resistant than those of others. A proportion of the infective larvæ of some species of roundworms parasitic in sheep and cattle can survive upon pastures for as long as eighteen months, and certainly there may be survivors of the larvæ of some species at the end of the winter ; but the numbers of these survivors will be different in different countries. Experimental work has shown, for example, that the infective larvæ of *Hæmonchus contortus* die in less than three months of hot, dry weather in South Africa, while in Texas they may survive for as long as 22 months. In eastern Canada and the Montreal area it was found that they did not survive from October until the following spring. Studies made at Beltsville, Maryland, in the United States, have, however, shown that in this region a few of the infective larvæ of *Hæmonchus contortus* may survive from the autumn until the following spring, but that the vigour and numbers of the survivors are usually not sufficient to enable this species to establish itself in sheep put out to graze in the spring. In Britain the climatic factors are so variable that it is likely that the infective larvæ survive for widely differing periods of time in different localities, so that it is difficult to say precisely how soon they will be killed on any particular pasture. While some experimental work which has been done suggests that the majority of them are killed in a few weeks in some British localities, farmers in other areas are disposed to give them a longer lease of life. The farmer wants to have as precise an answer as is possible to this question, because he wants to know how long he should leave infected land free from grazing sheep or lambs and how soon the risk of a heavy infestation can be ruled out. It is always difficult to answer this question, because so many factors have to be considered. It is not enough for the farmer to tell him that he should leave infected land free from sheep or lambs as long as he can. There has been during recent years a tendency to allow these animals to return too soon to infected land and the results of this practice have been, in some instances, disastrous. In Cambridgeshire farmers often leave land which has been contaminated by infective roundworm larvæ for as long as four years before it is grazed again, and this is undoubtedly a very wise policy if it can be adopted.

All the points of detail which have been discussed above will have emphasized the important part which biological studies play in the control of infestations with parasitic nematodes. Their bearing upon the control and effects of other kinds of parasitic animals is no less important. Many of the important advances which have been made in the control of the diseases of man and animals which are caused by parasitic animals have, indeed, resulted from the application of new information obtained about the biology of the parasites concerned. Advances in our knowledge of the principles of nutrition have also played a large part. The basis of good feeding is not the quantity of food, but the right amounts of the right kinds of foods. It is impossible, indeed, to overemphasize the importance of this factor, for good feeding—and especially, perhaps, an adequate supply of the vitamins—will provide the animal with two powerful means of defence. First, it will increase the natural resistance of the animal which develops when an infestation has been acquired and it will help to strengthen and maintain this. Second, good feeding will increase the resistance of the animal to infection with bacterial diseases. This is important, because the effects of these diseases may break down any natural resistance to roundworm infestations which has been acquired. A state of disease caused by roundworms will then be added to that caused by the bacteria. The effects of roundworms may, in a similar way, prepare the way for diseases caused by bacteria. It is, indeed, often difficult or impossible to say whether the initial trouble has been a bacterial infection which has enabled a roundworm infestation to increase or an infestation with roundworms which has enabled a bacterial infection to flourish.

The fundamental principles of the control of roundworm infestations must therefore be good feeding and wise management based upon our knowledge of the life histories of the roundworms concerned and upon a thorough knowledge of their relationships with their hosts. If these principles are applied, the average sheep will thrive, for we shall be helping it to establish that equilibrium between itself and its roundworm parasites which is the result of the normal forces of evolution. It is when this equilibrium is disturbed in such a way that the host suffers unduly that disease arises and our most economical method of preventing this from happening will be to study how nature ensures that both the parasitic animal and its hosts survive, and to do all we can to assist and maintain her methods of doing this.

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ANIMAL LIFE IN CAVES

By R. S. Hawes

CAVES are dark, damp, dirty and even, on occasions, dangerous places. The discomfort of exploring them discourages the inquisitive, and the muscular and athletic for the most part find more congenial outlets for their energies than trailing about subterranean chambers in which there is little to be seen and that only by artificial light. Only a few people enjoy climbing down long vertical shafts into the dark, clambering over sharp, uncertain rocks, and crawling along low, wet passages by the light of a carbide lamp ; of that few, only a small proportion consists of zoologists. Many of the densely populated caves of the world are in places remote from the ordinary amenities of civilized life and from such, for the zoologist, essentials as laboratories and libraries. No cave animals are of economic importance ; none causes disease in man or his domestic animals. For all these reasons it is not unnatural that, although a book on subterranean animals was written as long ago as the 17th century, our knowledge of the way in which they live, feed, behave and develop and of their precise relations to their peculiar environment and to one another is scanty, uneven and tantalizing. The elementary facts about the nature of the physical environment of many caves in Europe and America are fairly well known and numerous lists and descriptions of cavernicolous (*i.e.*, cave-dwelling) animals have been published. The general features of life as it is led in the darkness, the cold and the stillness of a cave are plain enough ; but they raise a number of obvious problems which require prolonged and detailed study before they can be solved with any confidence.

Caves vary greatly in size and formation. By far the most important to the naturalist are those which have been carved out from limestone rocks by a process in which the solvent action of carbonic acid, water erosion and the friction of sand and stones have all played their parts. The great cave systems of Southern Europe stretching from France to Palestine, in cretaceous limestone, and the caves of Virginia and Kentucky in the older carboniferous limestone, support a rich and diverse fauna of animals, highly specialized in relation to their long isolation in a unique environment. Such caves may form very extensive, ramifying systems of chambers and galleries, which are the deserted water courses of the streams and rivers which hollowed them out. This water has usually found a lower subterranean level, sometimes still in connection with the upper passages.

Just inside the cave, there is a region which is subjected to the same climatic conditions as those existing outside, but on a reduced scale. The alternation of day and night and the passage of the seasons, which dominate the lives of the animals outside, are still effective in the twilight zone near the cave mouth, though the fluctuations in illumination, temperature, humidity and so on, are less marked than in the open air. The extent of the twilight zone varies, depending on the structure of this part of the cave, but always, the farther from the entrance, the darker, damper, quieter and colder it becomes, and all conditions are less variable. The zone is of great importance, partly because it is one of the main links with the outside world, partly because it provides a kind of gradient of increasing approximation to conditions in the dark zone, up which the colonizers of the latter may pass and in which they may gradually acclimatize themselves. Some of the inhabitants of the twilight zone show a pallor and a tendency to have reduced eyes and elongated appendages, characteristics all found more commonly and more highly developed in the dark zone. The twilight zone insensibly passes into the dark zone beyond it and it is here that the typical cavernicolous fauna, such as is found in no other habitat, is established. The conditions of overriding importance are the total darkness, the low temperature and the very high humidity and stillness of the air. They are not only important in themselves but for their constancy, so that the animals suffer no seasonal change in their lives. The impenetrable darkness is absolute and has been unbroken for millions of years. The temperature is not only low, but always low; the water in Podpeška jama, in Jugoslavia, stood at 9.07 to 9.7° C. for two years ; there is a deviation of no more than half a degree from 9° C. in the depths of the great Grotte di Postumia on the frontier between Istria and Slovenia. The humidity of the air is commonly above 90 per cent, *i.e.*, the air contains more than 90 per cent of the maximum quantity of water vapour that it can hold. The silence is broken only by the faint dripping of water or the occasional splash of a fish. It will be understood that there are exceptions, some of which are mentioned below, but, in general, the cave environment is not only peculiar, but remarkably constant. Probably no other inhabitated places, except the cold, dark depths of the sea, present such a picture of, to us, inhospitable monotony.

The constancy of the major conditions does not preclude the differentiation of numerous distinctive habitats within the cave (Plates 1–8). The water present may be a roaring torrent, a gentle stream, a large, deep, calm lake, or in smaller pools and puddles, or in a tiny cup below a dripping stalactite. On land, the wet walls, smooth or cracked and furrowed, the stony or muddy floor, the pile of bat dung or the heap of decaying vegetation swept into the cave by a stream all provide habitats with their own peculiar features and each such "niche" is exploited by its own fauna. Such groups of animals are not isolated ; many species are common to several of them and there is a good deal of straying from place to place.

In spite of their specific and some adaptive differences related to their positions in the cave, typical cavernicolous animals commonly exhibit certain well marked characters. They are very often blind, or have eyes much reduced in size or efficiency, and as often they are colourless. The evolution of both characters has occurred independently in many groups ; blind, white amphibians, fishes, molluscs, insects, crustaceans, millipedes and eddy worms are all well known from caves, and even a white leech, *Dina absoloni*, has been found in Herzegovina. As if in compensation for loss of sight, organs of tactile sense, in which is included the means of detecting air currents, are often

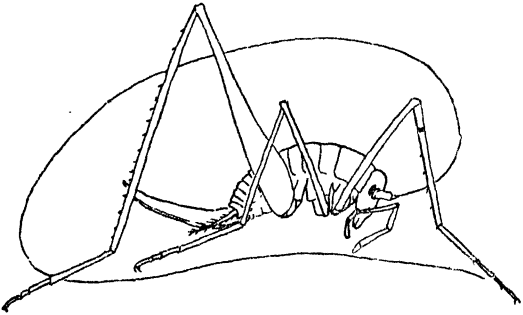


Fig. 1. *Dolichopoda bolivari*, a cavernicolous grasshopper. The colour is pale and eye reduced in size and simplified in structure. Note the elongated antennae and legs. After Chopard, modified. (By permission of Edition des Archives de Zoologie Expérimentale).

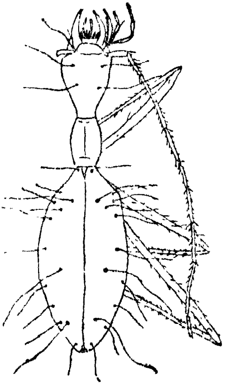


Fig. 2.

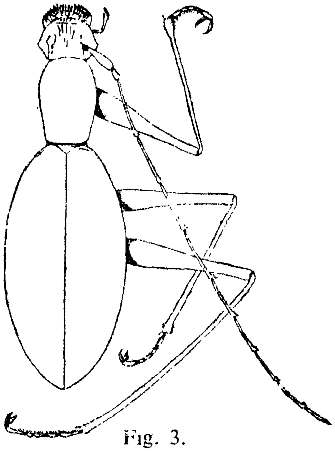


Fig. 3.

Fig. 2. *Aphaenops leschenautti*, a Carabid beetle from caves in the French Pyrenees. It is blind, unpigmented, and the antennae are unusually elongated. The long spindly legs are typical of the fauna found on the wet walls and sides of stalagmites. After Jeannel, modified.

Fig. 3. *Hadesia vašičecki*, a beetle from Herzegovinan caves. Although of a different family (Silphidae), *Hadesia* shows very similar peculiarities to those developed by *Aphaenops*. After Jeannel. (Figs. 2 and 3 by permission of M. Paul Chevalier).

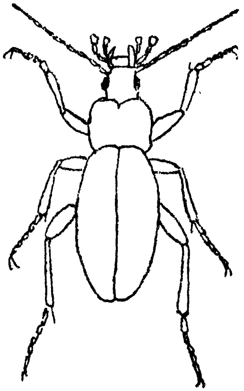


Fig. 4. A British Carabid beetle, *Corabus violaceus*, to show the normal length of the antennae and limbs in an epigean species. Compare with Fig. 2. (Redrawn after Joy. By permission of Frederick Warne and Co.)

highly developed. The normal stillness of the air within the cave creates an environment in which slight, small movements are more readily perceptible than in the open air ; not only is the sensory equipment for dealing with the phenomenon improved, but the nature of the environment enhances the stimulus. This type of structural modification is especially developed among insects, which may have unusually elongated antennæ or be covered with long, sensory "hairs" or setæ (Figs. 1 to 4). The aquatic animals are often drawn from groups already well equipped in this respect ; *Troglocaris*, the blind white shrimp of Balkan caves, has antennæ which, though very long, are comparable with those of many common shrimps. On the other hand, in *Niphargus balkanicus* (Fig. 5), related to the so-called brine-shrimps, a group normally provided with rather short antennæ, these organs have been extraordinarily elongated in relation to the creature's needs. A peculiarity

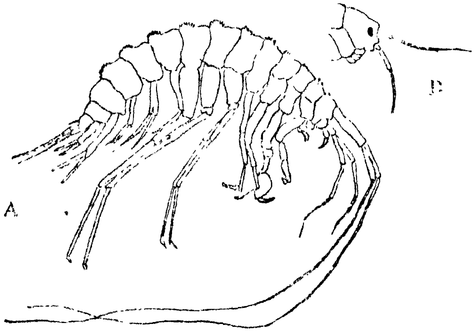


Fig. 5. (A) *Niphargus balkanicus*, a blind, white amphipod crustacean from Vjetrenica pećina in Herzegovina. The body is 2 inches long and it is the largest fresh water amphipod in Europe. *N. balkanicus* is found in pools such as those seen in Plates 3 and 7. After Absolon, modified. (B) The head of a British epigean amphipod for comparison, to show the eyes and normal antennae.

not fully understood and especially common among the insects living on the walls of caves is a tendency to develop very long, thin, spindly legs. It is well marked in beetles (Figs. 2 and 3) and gives them a peculiarly grotesque appearance.

It may seem at first sight surprising that so unpromising an environment should be inhabited at all. But it is the general experience of biologists that where life can be supported, life is found. Some of the surprise that caves are populated may be dispelled by the reflection that the gall bladder of a fish, the rectum of a frog and the blood stream of a lizard are all inhabited places. In one respect, caves are less inhospitable than is generally supposed ; though the food situation in them is unusual, there is plenty to eat, though it must come, in the long run, from the outside world: all animals directly or indirectly depend on green plants as the source of their food and there are no green plants in natural caves. A considerable quantity of vegetation is carried in by rivers and streams which flow for part of their courses overground. Heaps of dead and rotten wood and leaves and other organic débris are feeding grounds not only for numerous springtails, millipedes and some beetles, but also for the carnivorous beetles, spiders, phalangids and pseudoscorpions which prey upon them. Within the twilight zone, there is constant coming and going near the entrance, along the length of the zone, and between its deep end and the dark zone, and apart from these limited but overlapping excursions, the route is covered along its whole length by some animals, such as moths. All these regular wanderers, as well as the bodies of animals accidentally trapped in caves, contribute to the food stocks. Another most important food is bat dung, or guano. Some species of bats regularly hibernate in caves, and of these the gregarious members of the family Vespertilionidæ hang from the roof in great crowds. Below them lie sometimes vast accumulations of guano, supporting an elaborate association of coprozoic (*i.e.*, dung-eating) insects and their predators. It is a feature of the true guano eaters that they exhibit no specialization whatever in relation to cavernicolous life. The Staphylinid beetle, *Atheta subcavicola*, has normal eyes and wings and is pigmented like other species of its genus living outside caves ; yet it lives only within caves, breeds there and is unknown outside. The fly, *Phora aptina*, with similar habits, is likewise unmodified. Yet the numerous Carabid beetles which prey on the coprozoic species and their larvæ may exhibit pronounced specialization, *e.g.*, *Læmostenos navaricus*, a long, thin beetle, quite unpigmented, with greatly reduced eyes, is a characteristic cave animal in appearance. In addition, the guano supports a multitude of tiny Collembolid and Thysanuran insects, some Tineid moths which breed and pupate in the dung, terrestrial isopod crustaceans resembling the British woodlouse, cockroaches (though not in Europe), centipedes, which prey on all guanophiles, and even about a dozen species of snails. Finally, the larvæ of some of the beetles are heavily infested with parasitic mites. Although these different sources of food have here been separately mentioned, it is to be understood that there is constant communication between groups of animals benefiting from them, so that one supply contributes to the support of colonies to which it may not be directly available. Even the normal barriers between aquatic and terrestrial communities are less effective in caves than out of doors, as the humidity of the atmosphere diminishes them. The typically terrestrial isopod crustaceans like *Titanethes* habitually walk across the bottoms of pools in their paths and the aquatic amphipod crustaceans are able to wriggle over the damp ground from one pool to another.

The factors and events which have in the past been responsible for the initial colonization of caves were not the same for all species. Studies on the special needs and histories of different forms have not yet accumulated in sufficient quantity to permit extensive generalization, but a few examples well prove the diversity of the agencies at work. Aquatic animals are often swept into caves along with the water they inhabit and some of them there manage to survive. Minnows of the genus *Paraphoxinus* are not uncommon in European caves and seem to be none the worse for it. It is doubtful if *Paraphoxinus* can be regarded as anything but a typical epigean (above-ground) form capable of maintaining itself in cave waters, though it is just possible that in a slight reduction of its scales it is exhibiting the beginnings of a feature common in cave fishes. Be that as it may, *Paraphoxinus* demonstrates the possibility of accidental colonization without preliminary acclimatization, and the blind, white fishes of Cuban caves may have had some such origin. But for the most part cave animals are drawn from groups habitually living in damp, dim places, such as under stones or at the bottoms of streams ; they are, so to speak, preadapted to life in caves before they enter them. The operative factor in leading the animal into the cave may be humidity or the low illumination ; the two often go together in terrestrial habitats, so that their combination in caves presents no special difficulty. One of the commonest of all inhabitants of Balkan caves is the blind, white isopod, *Tithanethes*, related to the British wood-louse, *Porcellio*. The latter is found under stones or the bark of trees and requires a high degree of humidity for survival ; in dry air it is restless, loses weight rapidly and soon dies. Its habits ensure that it shall generally find a moist environment and it is easy to understand how such creatures would come to explore the entrance passages of caves ; *Porcellio* itself is common in the twilight zone and may penetrate into the dark zone. There is every reason to suppose that the ancestors of *Titanethes* first found their way into caves in this way. Another example in which humidity is the relevant factor in initiating colonization is provided by the giant long-horned grasshopper, *Dolichopoda* (Fig. 1). This and a related genus, *Troglophilus*, are the only two survivors of an ancient sub-tropical fauna of European Orthoptera dating from the Tertiary epoch. The element in this sub-tropical climate on which they depended was the high degree of humidity, not the heat, and when, in later periods, the European temperature fell and the air became dryer, *Dolichopoda* found in caves, though, paradoxically, they are cold, that moist atmosphere which alone can support it, and to-day its European range is confined to the cave lands of the northern Mediterranean and Adriatic littoral. It is occasionally met with out of doors, where conditions are suitable for it, but caves supply the only environment on which it can constantly depend for the maintenance of the humidity. As might be expected, the epigean relatives of *Dolichopoda* and *Troglophilus* are common in the warmer parts of the globe.

It is improbable that any animal living above ground can be attracted by or preadapted to total darkness, though the dim illumination of the twilight zone is experienced in other habitats, and by all nocturnal animals ; and an animal with habits that have accustomed it to dim light, may find darkness tolerable. The cave "salamander" of Istria and Jugoslavia, *Proteus anguinus*, though blind, is exceedingly sensitive to light and avoids it (Fig. 6). *Proteus* could not survive out of doors, and it was at one time thought that its reactions to light were adaptive devices developed as a means of keeping it within the safe limits

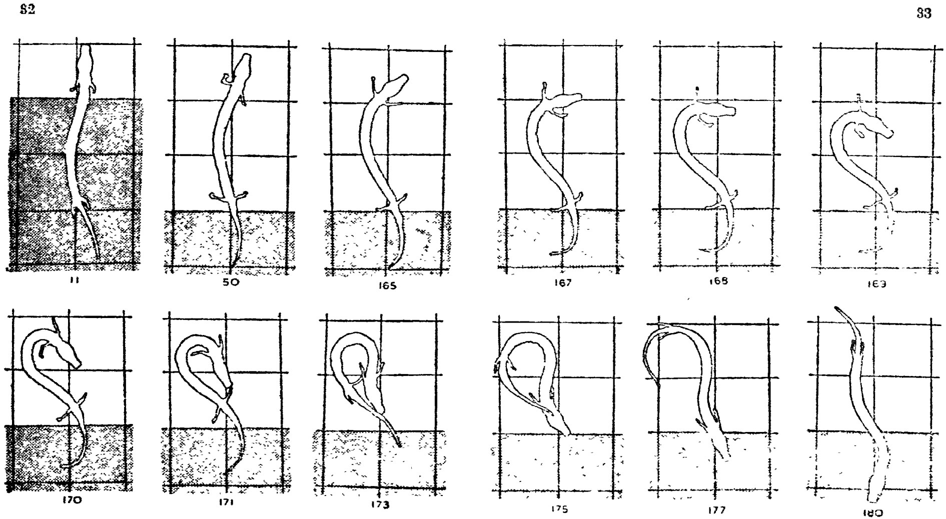


Fig. 6. The reaction of the blind, cave "salamander," *Proteus anguinus*, on passing from a dimly lighted area (shaded) to a strongly lighted one (unshaded). Each picture is traced from a frame of a film and the number beneath it represents the time in tenths of seconds, zero (not illustrated) being when the animal began to move in the dim area. At 5.0 seconds it was arrested in its path just after encountering the strong light and all movement was inhibited for the next 11.5 seconds, when, in a single movement lasting 1.5 seconds, the animal turned swiftly back into the dark. The reaction is very constant and does not depend on the tiny, vestigial eyes lying beneath the skin of the snout. (Reprinted by permission of Clarendon Press). *P. anguinus* lives in underground streams and lakes such as those shown in Plates 1 and 6.

of its cave. But clearly an animal living in total darkness has no opportunity of evolving a complicated set of reactions to a stimulus it never encounters and, in fact, the light reactions of *Proteus* must be thought of as an inheritance from its past life out of doors. Many other urodeles, *i.e.*, tailed Amphibia, retain their photosensitivity and continue to move away from light after their eyes have been removed. The nearest relative of *Proteus*, the mudpuppy, *Necturus*, of Carolina, is a bottom dweller in streams, where it lives in dimly lighted waters under rock ledges or among vegetation. Its habits are probably similar to those of the ancestors of *Proteus* when they lived above ground, and would account for their penetration into caves. What is surprising is the way in which the reactions of *Proteus* to light have kept, so to speak, in running order through millions of years of disuse.

It is easily seen that not all the physical factors in the cave environment are of equal importance in the lives of troglodytes. Some essential factor is present and the others, inseparable from it, are found tolerable; the latter may in time have a profound effect on the structure and habits of an animal to which they were in the first place irrelevant, or they may remain indifferent, neutral factors in the environment. *Proteus*, for example, habitually lives in water close to 9° C. in temperature; it has so lived for countless generations. Yet, provided that the change of temperature is slow and gradual, it can tolerate water as warm as 18° and will breed at 15° C. The coprozoic insects already mentioned are attracted to caves by the large stores of guano and their specialization is related to this alone; they could presumably live out of doors if they could find there the food on which they depend. *Troglophilus* shows no symptoms of dependence on any cave factor except moisture and is not uncommon in the woods outside, but

Dolichopoda, in which the eyes are somewhat reduced and the body pale, is probably beginning to evolve some degree of specialization which will eventually confine it exclusively to caves. For the most part, millions of years in the dark, the cold and the silence of the cave have left their mark on the inhabitants, and they are now unfitted for epigean life.

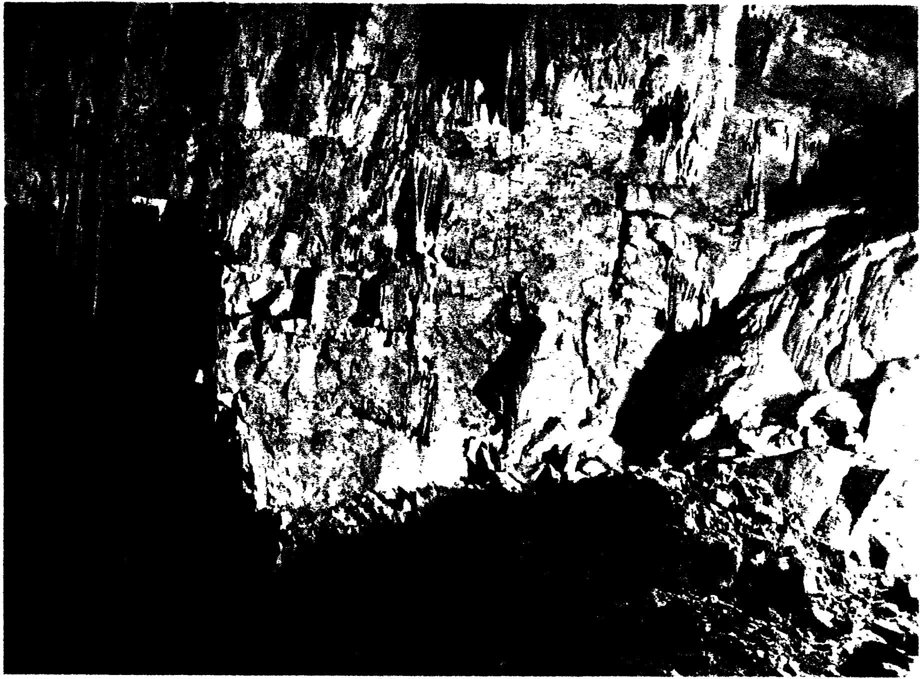
It is probable that the constancy of the environment should be regarded as a factor significant in itself, as distinct from the qualitative components of which it consists. This is to some extent reflected in the breeding habits of cavernicolous animals so far as they have been studied. In most animals, reproduction is restricted to periods of the year during which certain requisite stimuli are available. Where, as in the majority of caves, seasonal change is absent, there is a tendency for this restriction to disappear and the animals may breed throughout the year. Naturally, where a single variable factor is present, it may nullify the effects which might be expected from the constancy of the other factors. Some Dalmatian caves are subject to annual flooding, as the water from streams fed by the rains sweeps through them ; many galleries normally damp and supporting a typical terrestrial fauna are then inundated. At these times various fresh water animals such as sponges and polyzoans flourish normally under water. They survive the dry period within tough, resistant, capsules (gemmules and statoblasts) from which they emerge when covered again by the flood waters. Here, not only reproduction, but the whole active phase of the animal's life, in which it feeds and grows, is seasonal and alternates with a prolonged period of quiescence. Elsewhere, changes of humidity may affect the composition of the fauna, some species of beetles disappearing while others, tolerant of a wider range of humidity, are found throughout the year. Examples of such seasonal fluctuations are not very common, perhaps partly owing to the paucity of accurate records, maintained over long periods, of physical conditions in caves; it is possible that, as more detailed knowledge accumulates, some generalizations may have to be revised. But it is unlikely that the revisions will do more than emphasize exceptions to the general rule of constancy. The belief that this has had a marked effect on reproductive habits is supported by some, though admittedly limited, positive evidence. Common animals in the waters of European caves are blind, white amphipod crustaceans of the genus *Niphargus*, related to *Gammarus*, the brine shrimps of our own coasts and estuaries. When *Niphargus* is kept in aquaria at room temperatures, it breeds during the winter ; in the summer, when the temperature rises to 18° C., it does not reproduce at all. Its behaviour is similar in shallow wells, down to about 15 metres, where the temperature is affected by external conditions. But in deep wells, at 20 or more metres, where the water is always cold, young animals are found throughout the year, indicating that their parents can and do breed at all times. This is not an inherited or innate character of these populations ; adults from deep wells, when kept in aquaria subjected to thermal variation, breed only during the cold season.

In attempting to understand the evolution of the characteristics of the cave fauna, there are certain general considerations to be borne in mind. In the first place, it is an ancient fauna. If, on the map, we plot the southern limit of glaciation in Europe and America, we find that it roughly corresponds to the northern limit of the zone in which richly inhabited caves are distributed. In spite of some inconsistencies, the accuracy of the fit is very suggestive, and it implies that the cave fauna originated before the ice age and, in the northern regions, where it was destroyed by the advancing ice, it has not been replaced. We have already seen that *Dolichopoda* and *Troglophilus* have been more or less confined to caves since the end of the Tertiary. We are, then, dealing with a fauna which has been established in a highly peculiar environment for a very long period; there is no reason to think that in this time the environment has essentially changed its character, and there has therefore been abundant opportunity for the undisturbed development of a high degree of specialisation among the animals within it. To the force of this circumstance must be added that of isolation. During their long history, the inhabitants of caves have lived in a self-contained world protected against the effects of competition with the great majority of epigean animals. Characters which for the disadvantage they impose on their possessors would have been weeded out by the ordinary agency of natural selection within a normally constituted fauna may, in isolation, be retained. Finally, the unusual nature of the environment, itself calling for unusual characters in its inhabitants, need be no further emphasised. The combination of such factors would be expected to encourage the development of a highly distinctive fauna. To see the problem of evolution within the cave in proportion, the animals and their circumstances should be compared with those in some other inhospitable and strange habitat, such as a desert or the depths of the sea, where a high degree of specialisation typifies the fauna.

The most startling and the least intelligible of the characteristics of cave animals are undoubtedly their loss of pigment and eyes. The development of elongated antennae and other hypertrophied sensory organs is readily understood, for these are adaptive features of obvious value to the inhabitants of caves. But a similar explanation

1. The River Piuca in the Grotte di Postumia.

2. Lippertova Jama, Slovenia. The steel ladder can be rolled up and is portable.

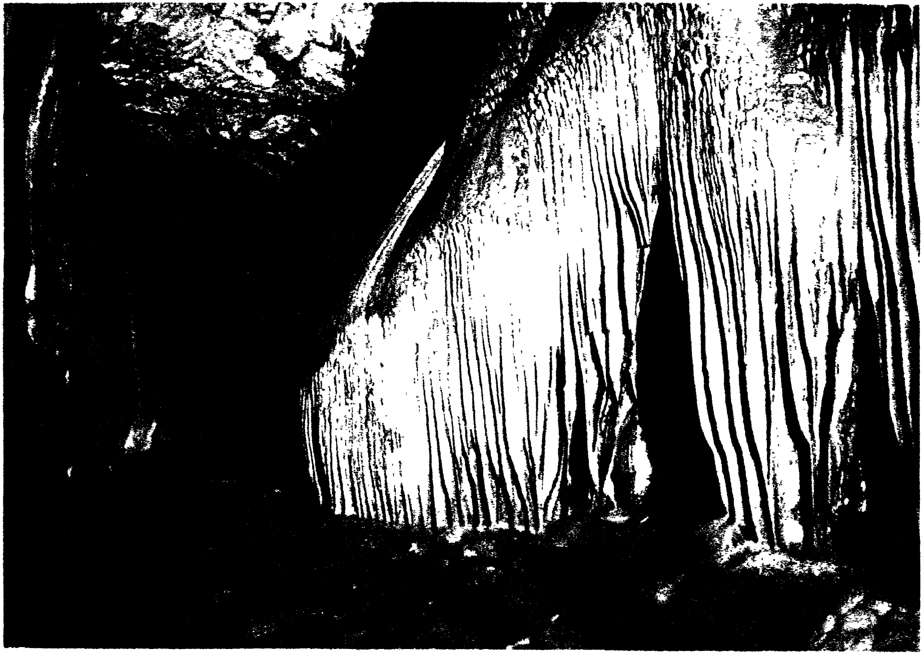


3. Pecina Vjetrenica. Herzegowina. The pools are the homes of the blind, white shrimp, *Troglocaris schmidt*, of *Niphargus* and other crustaceans.

4. Logarvek Brezno, Slovenia. The lamp is about 9 inches high. Note the moisture on the wall.

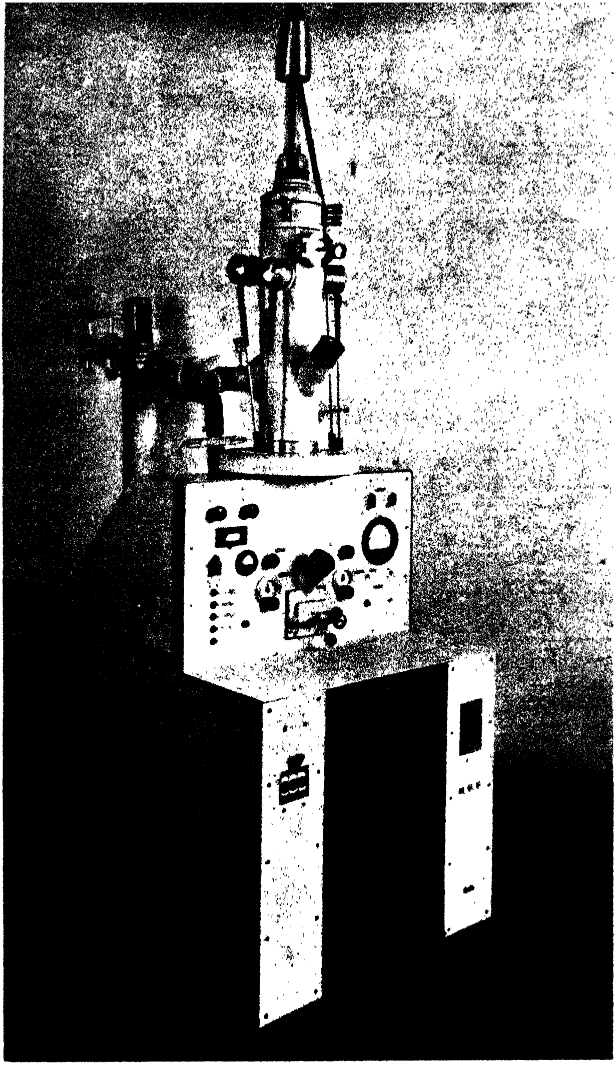
5. Krivna Jama, Slovenia. Mudbanks.

6. Krivna Jama, Slovenia.

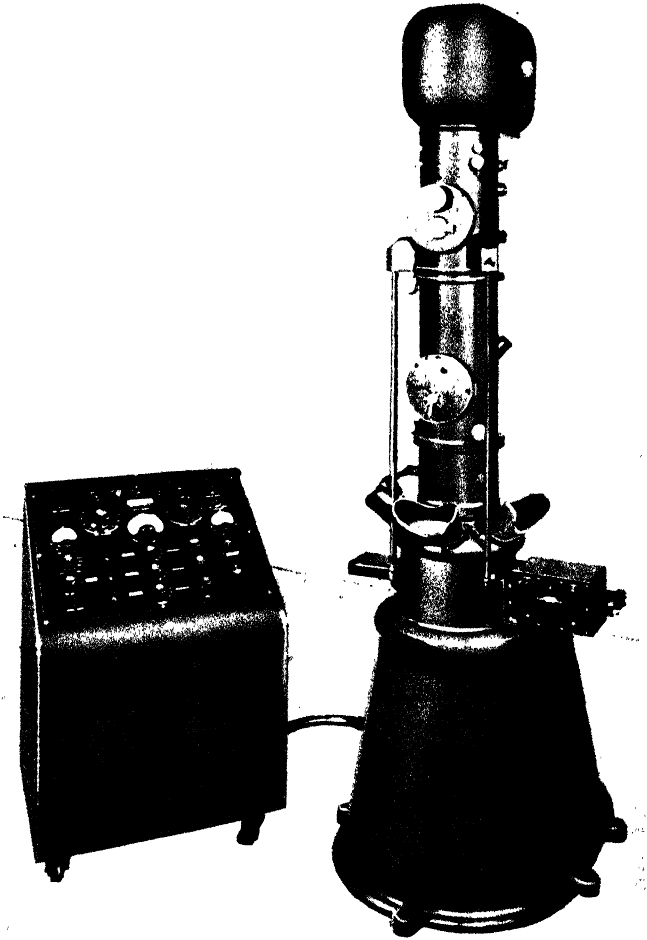


7. Vjetrenica Pecina,
Herzegowina.

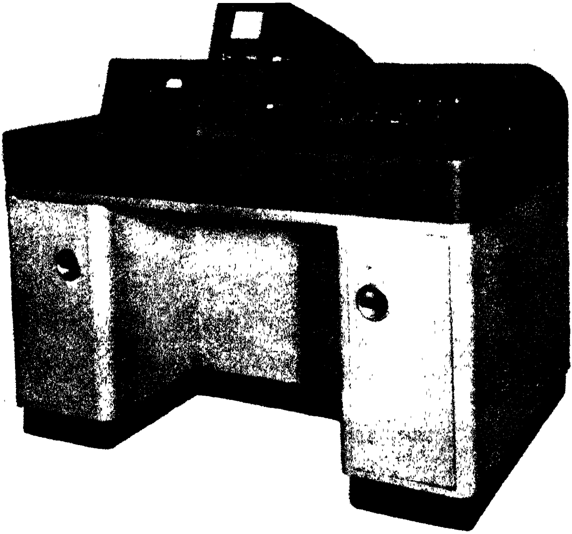
8. Logarvek Brezno,
Slovenia



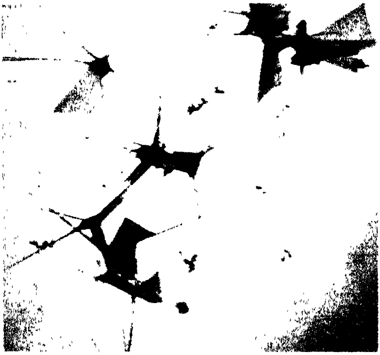
9. Magnetic electron microscope (Metropolitan-Vickers).



10. Electrostatic electron microscope (Bruck and Grivet, Paris).

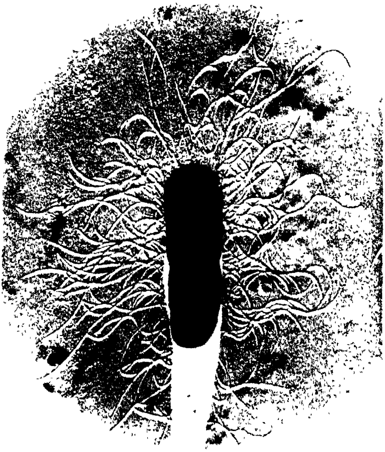


11. Desk-type electron microscope (magnetic). (Radio Corporation of America).

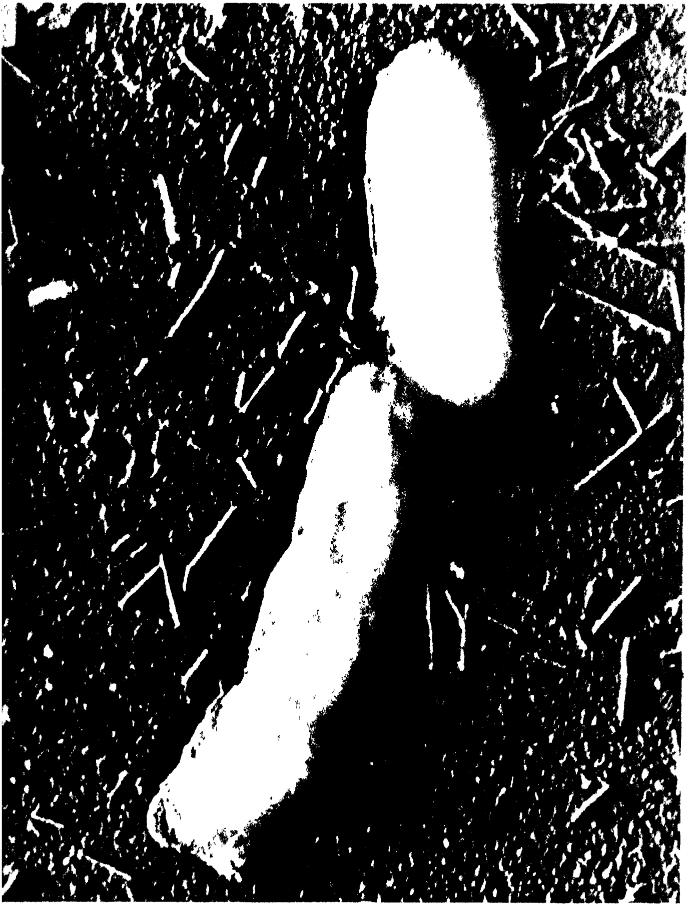


12. Particles of very fine smoke of Zinc Oxide. Magnification 11,000 times (Miss Tilleard. Paint Research Station).

13. Caryophanon bacillus (the black object in the middle with white shadow), showing whip-like projections (flagella) by which it moves, made to stand out clearly by the technique of gold shadowing. Magnification 8,000 times (Drs. C. R. Robinow and G. R. Crowe, Cambridge).

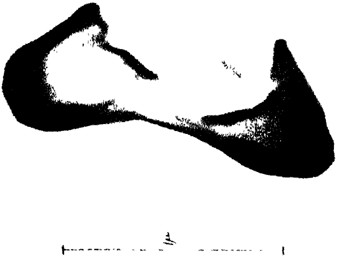


14. Germ (Rickettsia) of epidemic typhus, showing internal structures. Magnification 18,000 times (J. Smiles, National Institute of Medical Research).



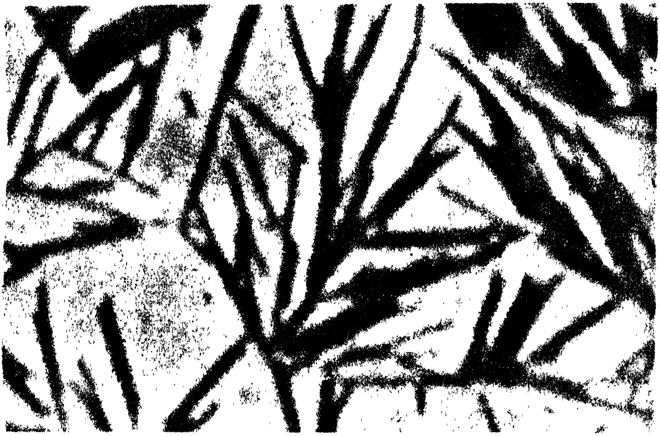
15. Bacilli (unidentified) shadowed with gold to show surface form, with tobacco mosaic virus particles for magnification estimation. Magnification 36,000 times (Dr. R. Reed, Leeds).

16. A bacterial spore in the process of germination. The bacterium has been caught issuing forth from the spore case (Bacillus cereus). Magnification 14,000 times (Drs. C. R. Robinow and G. R. Crowe, Cambridge).



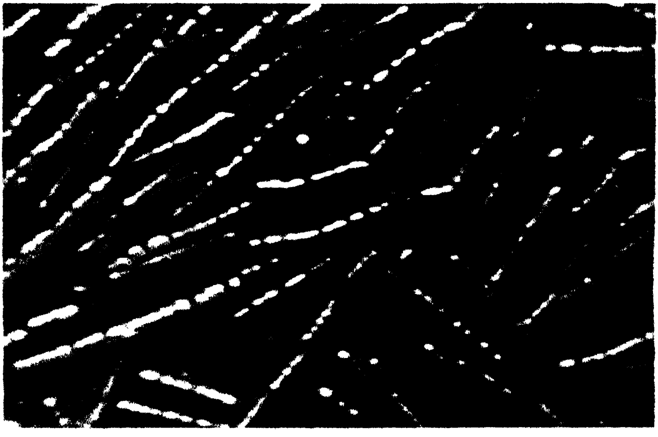
17. Discarded spore case of a bacterium (Bacillus mesentericus). Magnification 30,000 times (Drs. C. R. Robinow and G. R. Crowe, Cambridge).

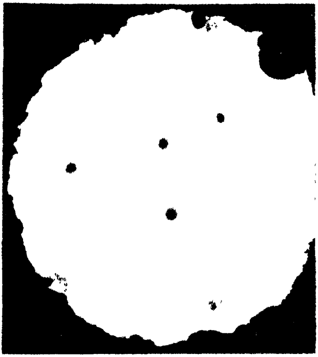
18. Staphylococci (three large black spheres) and a bacteriophage (53K) which attacks them (small dots). (Dr. Lepine, Institut Pasteur).



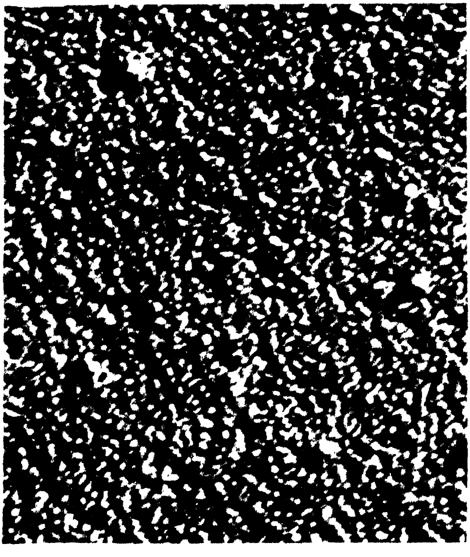
19. A virus (Tomato Aucuba Mosaic). The virus particles are rod-shaped, and variously aggregated together. Magnification 70,000 times (Drs. K. Smith, Markham and G. R. Crowe, Cambridge).

20. Same as Plate 19, but shadowed with gold, to show how this technique brings out otherwise invisible surface markings. Magnification 70,000 times (Drs. K. Smith, Markham and G. R. Crowe, Cambridge).

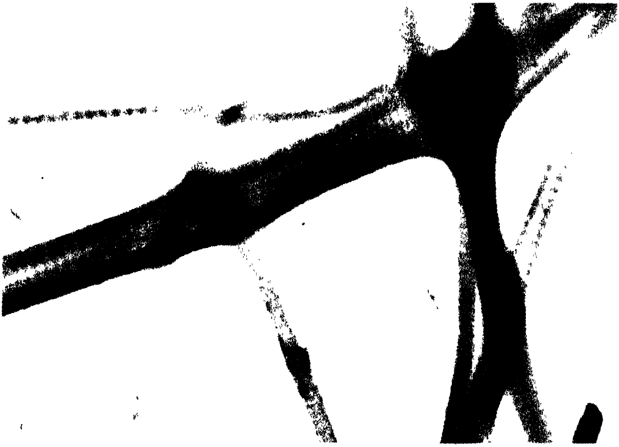




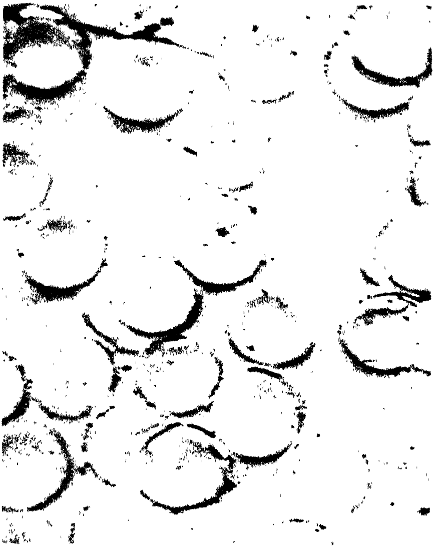
21. Bacteriophage (subtilis), showing dense round head and narrow tail. Magnification 35,000 times (Dr. Lepine, Institut Pasteur).



22. Individual molecules (of haemoglobin from a pond-snail), shown up by gold shadowing. Magnification 70,000 times (Drs. K. Smith, Markham and G. R. Crowe, Cambridge).



23. Connective tissue (collagen) fibrils, showing striations unknown before electron microscopy. A staining method has been used. Magnification 25,000 times (Dr. R Reed, Leeds).



24. Replica of red blood cells, obtained by polystryene-silica method (see text). Magnification 1,500 times (Drs. Barnes, Burton and Scott, American Cyanamid Co.).

cannot be applied to depigmentation and blindness, which confer not the slightest benefit on their bearers.* Some attempt has been made to include depigmentation within the scope of the theory of natural selection on the ground that failure to produce pigment effected an advantageous saving of energy; the attempt is hopelessly doctrinaire and no one has ever seriously considered that the energy required to produce pigment made any significant difference in the general metabolic economy of any animal. Before going on to suggest another explanation, it will be well to outline some of the salient facts about the pigmentation of cave animals.

Although a great many cave animals are unpigmented, they exhibit the effects in different ways and even when they appear alike they may have achieved a similar state by different means. The following are among the most important variations:—

1. Animals ordinarily living above ground, where they are normally pigmented, may lose some or all of their colour if exposed for some time to the dark. In a trout recorded in 1931 from a German cave, where its occurrence was undoubtedly accidental, a good deal of the melanic pigment was lost, with resulting pallor, and the reddish spots of carotin had completely disappeared. Two young fishes of the species *Squalius cephalus*, found in the depths of the Grotte di Postumia, were quite white. In both cases, the modification had almost certainly taken place within the lifetime of the fish.

2. Some cavernicolous animals are normally colourless, but develop ordinary pigmentation when exposed to light.

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* By adopting the Lamarckian view that the effects of disuse are inherited, it is easy to explain the loss of eyes, though perhaps not that of pigment. But most biologists now reject Lamarckism and the explanation offered below is in terms of a more generally accepted theory; but it is not to be supposed that the modern Lamarckian theorists are, because in a minority, necessarily in error.

Proteus anguinus in nature has a colourless integument, with blood-red gills and two tiny black spots on the head, which indicate the position of the greatly reduced eyes beneath the skin. One delicate layer of tissue about the remains of the eye retains its capacity to produce pigment in the dark; everywhere else in the body this has been lost. But if *Proteus* is kept in the light, its skin slowly darkens and finally achieves a deep grey colour; in spite of its long history in darkness, it can still produce pigment when illuminated, though this activity of the skin is never exercised in nature.

3. Of great importance to the argument developed below are some of the cavernicolous beetles which, though they have lost all their body pigment, fail to exhibit the effect. The colour of the hard, chitinous exoskeleton which encloses them is developed separately from that of the body. Normal coloration is a combined effect of the two, but in the cave beetles the body pigment is lost and the flesh colorless, while the chitin retains its colour, so that to the eye, the beetles appear reddish brown.

4. Finally, there is the great class of cavernicolous animals which have irrevocably lost all capacity to produce pigment and appear white. The majority of cave crustacea are included here, such as *Titanethes*, *Troglocaris*, *Niphargus* and hosts of minute and lesser known forms. The whiteness of these animals is genetic, *i.e.*, established as an innate, inherited character.

The problem is to explain how the white character has come to be inherited throughout extensive populations of many different animals. To grasp the point of the explanation, some preliminary digression on the nature and acquisition of inherited characters is necessary. It is well known that in populations of organisms with well defined characters, heritable variations may spontaneously appear which cannot be explained as the results of recombinations of existing genetical factors. Such mutations, as they are called, are, in fact, novelties; how they arise is uncertain, but once they have appeared, they are inherited in the same way as pre-existing characters. It is further maintained that mutations conferring even very slight advantages on their possessors tend to spread throughout the population, while those which are disadvantageous are selected out. That some such explanation underlies the evolution of all adaptations cannot be regarded as proven, but it is nevertheless a highly simplified version of an explanation which, most zoologists would admit, can be applied to the majority of carefully investigated cases. It is important to understand that the value of a character which determines its fate can generally be assessed only in relation to the environment; what is useful in one place, is harmful or neutral elsewhere. Now, nearly all mutations are deleterious; it is a point emphasised by those who are most opposed to the genetical theory of natural selection here outlined, and it is easily intelligible. Most characters in any organism are not simply produced, but result from the complex interaction of a wide variety of agencies operating in a harmonious system. It is highly improbable that any random modification of a part of such a system can be advantageously incorporated in it as a whole.

The production of pigment is itself just such a complex system as is more likely to be impaired than improved by alterations arising haphazardly within it. Under natural conditions above ground, such imperfections of pigmentation resulting from mutation would normally be weeded out. The coloration of an epigean animal with a well established pigmentary pattern having such a genetical basis may be conceived as an elaborate device which is constantly tending to break down, but is maintained in its normal state by the pressure of natural selection. But among blind animals living in the dark, coloration is valueless and meaningless; alterations of pattern confer no advantage or disadvantage, but are neutral. In the absence of the ordinary basis of selection pressure, the pigment-producing mechanism would tend to degenerate. There need be no doubt that loss of eyes and pigment are related to the darkness and to no other factor, such as temperature; a completely blind, white crustacean has been found in the dark recesses of a hot spring near Tunis, where it lives at a temperature of 45° C. If this argument is anything more than plausible speculation, it should be possible to collect supporting factual evidence. The instability of pigmentation should lead to the production of individuals with abnormal coloration; they would be observed only rarely in nature, but more commonly in populations maintained artificially in the laboratory. Secondly, the pigmentation of cave animals should be a demonstrably negligible factor in their lives. Thirdly, one might expect to find that animals in the process of colonizing caves and closely related to epigean species would show great variability in coloration. Some evidence is available under all these headings.

(1) Noticeably pale animals would not survive long in wild populations above ground, but are occasionally reported. Unpigmented isopod crustaceans (*Porcellio laevis* and *Asellus aquaticus*) are, though rarely, collected in nature. In laboratory-bred populations, they are commoner. The isopod, *Armadillidium odhneri*, collected in the Riviera and reared in the laboratory, produced a number of unpigmented, light-eyed individuals in each generation; mutations for reduction in pigment occur in laboratory-bred stocks of the amphipod, *Gammarus chevreuxi*. (2) That pigmentation is really meaningless in the

dark might seem obvious enough, but two sets of supporting facts may be quoted. Careful examination of populations of some unpigmented cave animals shows that they are sometimes less uniform than generally supposed; the blind fish *Stygicola dentatus*, within its native caves, is not always white, but may be pale or even deeply pigmented, and no disadvantage seems to attach to the coloured individuals. More important is the group of insects which, although they lose their melanic pigment, retain the coloration of their chitin. Their loss of pigment is masked by another character, but ineffectiveness of the modification has not hindered its spread. As explained above, quite normally pigmented beetles are common in guano, side by side with unpigmented species. (3) The common British and European "water louse," *Asellus aquaticus*, an isopod crustacean, is, above ground, normally pigmented. A number of species of *Asellus*, confined to caves, are blind and white, but *A. aquaticus*, when, as in Istria, it penetrates caves, exhibits great diversity of coloration. Every transitional stage from complete depigmentation to normal coloration is found and all types of individuals live side by side. When bred in captivity, the offspring exhibit a similar diversity of pigmentation. These populations illustrate not only the insignificance of colour mutations in darkness, but their variety. Such a gradual tendency to achieve whiteness by interference with different stages of a complicated process is, of course, distinct from the well known albino mutations, in which, by a single skip, complete depigmentation is at once effected.

A similar argument can be applied to the degeneration of the eye, which is one of the most complicated of all organs. Heritable imperfections of vision of many different types are well known, especially in man, where they have been most closely studied. In cave animals, the occurrence of different kinds of eye degeneration strongly suggest that the constant tendency to produce destructive mutants affecting visual efficiency in various ways is expressing itself unchecked in an environment which permits the preservation and spread of heritable deficiencies in a useless organ.

It is to be repeated in conclusion that, if the broad outlines of the natural history of caves are apparent, the details are lacking. What we already know reveals a complex picture in need of further analysis. The fauna is derived from many different sources; animals have been carried passively into caves by fresh water streams to die or survive there according to their natures; some have migrated slowly, gradually, by processes unknown to us, from the sea; others, with habits predisposing them to explore the damp, dim, cool area of the twilight zone, have found safety there and subsequently exploited the recesses of the dark zone. Accident, the conditions of illumination, humidity, temperature, and even food, have acted as effective attractions to colonizers, but once within the cave the inhabitants have been exposed to all the agencies present and their responses have been varied. Many have become so specialised that they cannot survive outside their caves. Such a story is in fact far more complicated than an essay on it can imply; it must be remembered that all simplification distorts. What is needed is more detailed study, over long periods, of the relations of cavernicolous species to each other and to their environment and such investigations, to be fruitful, would require support from much experimental investigation into the physiology, development and genetics of cave animals. The technical and other difficulties in the way of such progress are often very great and the material inducements to overcome them slight; small bands of enthusiastic workers, like those who laid the foundations of biospelaeology, can hardly be expected to produce rapid results in wide fields of research calling for the organised resources of great institutions.

FURTHER READING

There are no good, general books on cave animals in English. Easily the most vivid and stimulating accounts of life in caves are Jeannel's "Faune cavernicole de la France," Paris, 1926, and the same author's "Les fossiles vivants des cavernes," Paris, 1943. They have little to say of aquatic forms, which are dealt with by Spandl "Die Tierwelt der unteriridischen Gewässer," Vienna, 1926, and a book of the same title by Chappuis, 1927.

THE ELECTRON MICROSCOPE AND BIOLOGICAL RESEARCH

By V. E. Cosslett

1. *Introduction.*

If one glances casually at the illustrations in the newspapers, one has the impression of continuous gradations of light and shade, as in an ordinary photographic print. Close inspection, however, reveals that the picture is in fact made up of a great number of regularly arranged black dots, the size of which varies from point to point according to the corresponding density in the photograph from which it was made. At arm's length the illustration appears quite continuous in shading, but at short range the separate dots are visible: the "resolving power" of the eye has been increased by bringing the paper nearer sufficiently for the details to be distinguished. Thus the *resolving power*, or *resolution*, of an optical system, be it a microscope, telescope, or the human eye, is the *power of discriminating detail* in an object. It is defined as *the least distance which two points have to be apart if they are to appear to be separate.*

In the design of an optical system it is most important to ensure that the resolving power is increased whenever the magnifying power is increased. If this is not so, then a larger magnification will simply give larger versions of the blurs which were visible already, without showing finer detail within them. Fortunately it is usually not difficult to improve both resolving power and magnification together.

The resolving power is determined by the amount of light gathered by the lens nearest the object, and also by the wavelength of the illumination. By bringing a news-paper picture closer to the eyes we are increasing the amount of light gathered from the object, since we are increasing the size of the cone of light entering the eye from any individual point in the picture. The size of the cone is given by the diameter of the viewing lens divided by the distance it is from the object: this is called the *effective aperture* of the eye. High resolution thus demands a wide viewing aperture—a large lens at a distance from the object (as in the telescope), or an object very close to a small lens (microscope). Resolving power is also determined by the wavelength of the illumination, since the light rays will get around any minute objects which are smaller than their wavelength and thus fail to give corresponding differences of contrast in the visible image.

It is some 300 years since the optical microscope appeared in the world—discovered, rather than invented, by the chance arrangement of two spectacle lenses. The early instruments suffered from defects which seriously interfered with their resolving power, particularly from severe spherical and chromatic aberration, and it has taken a long process of trial and error, supplemented more recently by scientific investigation, to perfect the optical system.[1] In the modern optical microscope the lenses are so perfectly designed that spherical and chromatic aberrations are negligible, effective aperture is maximal, and *the sharpness of the image is limited only by the wavelength of light itself.* It is impossible to observe with a microscope any details which are much smaller than the wavelength of the illuminating light; the instrument has a definite "resolving power" determined by the latter, and not by any physical imperfections of its optical system. Thus we cannot hope for significant further advance from the optical microscope.

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[1] *Sperical aberration* arises from the inability of a spherical lens surface to bring to the same focus rays which enter it at different distances from its axis, so that the periphery of the lens is a hindrance to the formation of a sharply focused image. This defect therefore limits the amount of light which can be usefully gathered by a lens from a particular point, *i.e.*, the effective aperture of the lens must in practice be made small. Correction for it is provided by making a combination of lenses, using different kinds of glass of varying optical properties. *Chromatic aberration* leads to a similar lack of sharp focus, but now arises from the inability of a lens to bring light of different colours (that is, different wavelengths) to the same focus, even when all the entrant rays are at the same distance from the axis. It is also in large degree corrected by the design of compound lens systems, when it is desired to use ordinary white light as illumination. Alternatively, of course, light of a single wavelength (monochromatic beam) may be employed, as in the ultra-violet microscope, and the aberration thereby eliminated.

The electron microscope improves upon the performance of the light microscope because the equivalent wavelength of the electron beam employed for illuminating objects is very much smaller than that of light. It was invented in 1931-32, being developed upon the highly theoretical hypothesis of de Broglie regarding the wave-nature of the electron, which was first propounded only seven years earlier. It was a triumph for the complex analysis of fundamentals and the detailed development of electrical engineering, which comprise so much of modern applied physics. The first instruments were seriously afflicted with spherical and chromatic aberrations (and hence were limited to small effective apertures), so that the full possibilities of improved resolution could not be immediately realised. The wavelength of the electron is, however, so many thousand times smaller than that of light that the resolving power of the ordinary microscope was soon exceeded by ten times, even when using apertures 1,000 times smaller than in the former; in recent years a further advance of ten times has been achieved. Considerable progress has now been made in overcoming the "chromatic" error, which arises in the electron microscope as in the light type, since electrons also have various wavelengths: it is countered by providing an electron beam of highest possible uniformity of wavelength, *i.e.*, produced by a high-voltage source of great stability. Some advance has also been made in countering spherical aberration, but in electron optics the same slow advance to perfection as occurred in light optics is likely to be repeated, speaking relatively to the higher general level of physical knowledge. It may require as long as 30 or 60 years before the full potentialities of the electron microscope are realised.

The limit of resolution of the optical microscope, *i.e.*, the size of the smallest visible detail, is about one-third the wavelength of the illuminating light: roughly 2000A ($=0.2\mu$) for yellow light, or 1000A for ultra-violet light. (An A or Angstrom is one ten millionth of a millimetre; a μ or micron one thousandth of a millimetre). The wavelength of an electron beam accelerated by a voltage of 60 kV is as small as 0.05 A, or roughly 20 times smaller than atomic dimensions. An electron microscope with perfectly corrected lenses would, therefore, be expected to have a resolving power less still than this figure. The best results so far achieved (Hillier) are of the order of 10 A; the commercially available instruments (Siemens, RCA, Metropolitan-Vickers) have a resolution of 50–100A.

It is clear, therefore, that although the new microscope is in its infancy, it has already far surpassed the limits of the optical instrument, and, although much of the work so far done with it has been frankly exploratory only, it has already added considerably to scientific knowledge. It can be used in every field where its optical counterpart works with transmitted light, providing that specimens can be prepared of sufficient thinness to transmit the major part of the electrons. The rapid development of new techniques, especially that of the high-speed microtome (see below) already begins to make the two fields co-extensive as well as complementary. It is the purpose of this article to indicate the possibilities of electron microscopy, especially for biological investigations, and also its major limitations. On both accounts it is necessary to start with a short description of the instrument itself, and the principles of its operation.

2. *The Electron Microscope.*

The electron microscope follows in general lines of construction those of the light microscope: it has an illuminating source, a *condensing lens* to focus the illuminating beam, an *objective lens* for primary magnification and then a succeeding lens (called the *projection lens* in the electron microscope) for forming the final image. The essential difference lies in the use of electrons instead of light for illumination, and this has so many consequential effects that the finished instrument bears little resemblance to the well-known layout of the high-powered optical microscope.

Light is a wave-motion which in certain circumstances displays corpuscular properties. Certain solid materials are almost completely transparent to it, and differences in physical density and chemical composition between successive media (*e.g.*, air and glass, in the case of an ordinary lens) cause a bending (refraction) of a light beam. On this fundamental fact is founded the possibility of making lenses to focus light, and hence of constructing a microscope. Clear images may be obtained by making the lens surfaces spherical in shape; the use of two lenses in series produces two successive enlargements in the image, and constitutes a microscope. Electrons, on the other hand, are particles which in some sense have a wave associated with them ("guiding" them). They are readily scattered and absorbed by all forms of matter, and optical lenses cannot transmit, let alone focus, an electron beam. This can be done only by making use of the fact that charged particles can be deviated by electromagnetic fields: a field of properly designed form can focus electrons in essentially the same way as glass lenses focus light. The necessary fields can be set up by special arrangements of magnets, by producing magnetic fields in current-carrying coils, or by charging suitably shaped metal electrodes to different voltages. In principle both electric and magnetic methods can be used together, but practically it is more convenient to employ either purely electric or purely magnetic lenses. The most successful microscopes, so far, employ the latter.

Fig. 1, then, shows the construction of an electron microscope in schematic form, the lenses being indicated merely by a few lines showing the focussing fields. These lines stand for the shape of the equipotentials in electrostatic lenses, or for an equivalent potential (not for the lines of force) in magnetic lenses. The general shape is reminiscent of the biconvex lenses of glass optics. It may be noted that any type of charged particles can equally well be focussed by such fields, as well as electrons. A proton microscope is perfectly feasible, and is now in process of construction in Paris. Ion microscopes have also been constructed, and recognisable images obtained with them (Boersch).

The illuminating source of the electron microscope must be a powerfully emitting cathode, usually a white-hot tungsten hairpin. The whole of the beam path must be in vacuo, since electrons are readily absorbed and scattered from the beam by a very small amount of air, and therefore the instrument must be air-tight and continuously evacuated through high-speed pumps. On this account, and also because electrons are in any case not registered directly by the human eye, the enlarged image is recorded on a photographic plate, after being observed in the form of its

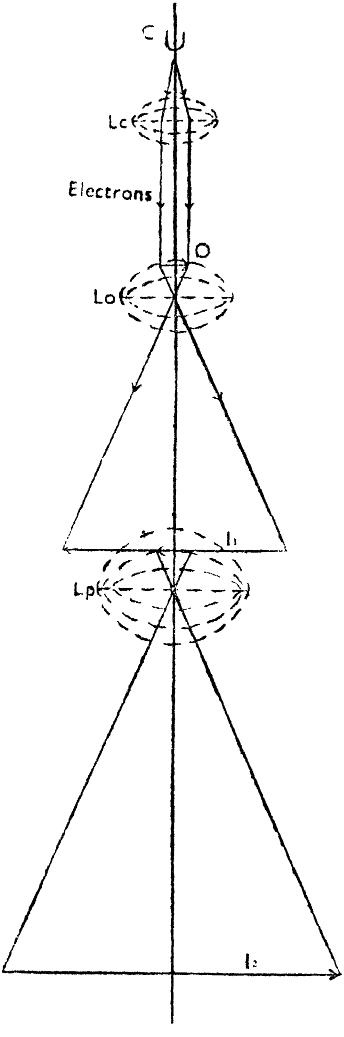

Fig. 1. Electron Microscope: An illuminating beam of electrons, from the cathode *C* and condenser lens *Lc*, falls on the object *O* immersed in the field of the objective lens *Lo*. which forms an image *I1*; part of this image is further enlarged by the projector lens *Lp*, giving a real image *I2* on screen or plate.

fluorescent counterpart produced by impact of the beam on a zinc sulphide or similar screen, as in the ordinary television tube. There is ample depth of focus in the image for the focussing on the screen to be the same as on the plate which is subsequently exposed behind or in front of it. Photography of the fluorescent image from outside the instrument is possible, as in the cathode ray tube, but is inadequate for high resolution owing to the broadening of the image points first in the fluorescent material itself and then in the backing glass.

Enough will have been said to make clear the main similarities and points of difference in the general construction of the light and electron microscopes. In this short space no attempt will be made to describe the detailed construction of one of the latter type; full accounts will be found in any of the recent technical books (references 1, 2 and 3). A photograph of a magnetic microscope is shown in Plate 9, and one of an electrostatic type in Plate 9. *They stand some 6 to 7 feet in height and in both cases have a certain amount of the electrical and pumping equipment in separate cabinets, or even in a separate generating room. They cost some thousands of pounds to construct. The chief exception to these statements is the desk-type magnetic microscope lately developed by the Radio Corporation of America, which incorporates all the necessary gear in the pillars and rear of a desk of normal size (Plate 11), apart from the rotary oil-pump. The objective and projection lenses are here incorporated into one lens-unit. It gives a best resolution of 100 A at a magnification of 5,000, as compared with about 50 A at a magnification of 20,000 to 40,000 in the vertical types.

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* The plates showing these microscopes are wrongly numbered. The caption of plate 9 should be read with plate 10, and vice versa

3. *Image Formation.*

There are several important differences in regard to the process of image formation between the electron and optical microscopes, and as these affect the uses and operation of the former, they must be briefly indicated.

In the optical microscope, the detail of the image arises primarily from differential absorption in the specimen, which is often so transparent to the illumination that special stains have to be used to render different structures visible in it. The specimen is comparatively thick (from several μ to the order of a mm.). On the contrary, the primary interaction of matter with an electron beam is that of scattering. A dense particle in the path of the beam will absorb some electrons but will scatter very many more, that is, will deflect them through an angle so that they do not pass through the aperture of the lens along with the main beam, which subsequently forms the image. The apertures used in present electron lenses are so minute that this scattering is very effective in removing electrons when the beam encounters dense regions in the object; the image then shows a corresponding lack of electrons at these points, causing light patches in the negative and dark patches in the positive print. If the specimen is too thick, then there is a high chance that scattering will occur somewhere in all parts of its cross section as the beam goes through. Hence it results that only extremely thin specimens (by optical standards) are permissible, of the order of 0.1μ and less. The use of the electron microscope is thus limited to the examination of specimens which are themselves smaller than 1000 A in dimensions, or which can be cut in sections of this size by special microtomes (see below, p. 122). It also follows that optical stains cannot necessarily be of value in electron microscopy, as they may have the same scattering power as the tissues in which they are absorbed. A new staining technique has to be learnt, largely by trial and error, using materials of greatly differing mass density from their surroundings (see p. 123).

In the optical microscope the depth of focus is of the order of a fraction of a micron (μ), with the result that only a very small cross section of the specimen is in focus at one time. This has the advantage of allowing detail to be isolated in a thick specimen, but the disadvantage that it is not easy to find any desired feature, the whole specimen having to be searched layer by layer by axial motion of either stage or microscope. In the electron microscope the depth of focus is about 1000 times the limiting resolution and thus of the order of a micron—or greater than the permissible thickness of the specimen. As a result, the whole of the specimen in depth is in focus at once in the final image. This allows rapid exploration of specimens, the relative position of object and lenses remaining constant, but is apt to conceal refinements of detail unless sections can be cut of a thickness of nearly the same order as the detail sought; this is likely to remain impossible in the region of limiting resolution, since it is unlikely that sections thinner than 100A can be cut by any method.

In operation, the objective lens is used to obtain fine focussing, at roughly fixed magnification, whilst the power of the projection lens is varied in order to change the overall magnification. No axial manipulation of either object or lenses is necessary in the magnetic microscope, nor is it necessary to change the objective when the magnification range is changed. This facility of operation rests upon the fact that electron lenses share the ready accommodation of the eye, but in infinitely greater degree. Simply by varying the exciting current flowing in the coils of the electron lenses, the strength of the magnetic fields produced can be varied from almost zero up to the limits set by the properties of the iron pole-pieces. The flexibility in this sense of the electromagnetic field offsets in some degree its lack of amenability to correction of spherical and chromatic aberration, and makes the electron microscope a very simple instrument in operation, as distinct from its construction and servicing.

4. *Limitations.*

Before proceeding to describe the various applications to which the electron microscope has been put, it will be as well to make clear the chief limitations on its use. These are to a large extent inherent in the physical principles of its construction and operation, which have been dealt within the previous section. But it will be helpful to summarise the limiting factors here, especially with reference to biological specimens.

(*a*) The existence in the electron lenses of spherical aberration, and to a lesser degree of chromatic aberration is the main limitation on the resolution which can be attained in microscopes of present design. It results in a resolving power of tens of Angstrom units, instead of the tenths which should be allowed by the minute wavelength of the electron beam.

(*b*) The ease with which electrons are scattered produces high contrast in the images, but also limits observation to specimens much thinner than those employed for optical microscopy. The "transparency" of materials to electrons is very low, and specimens must be thinner than 0.1μ for good results to be obtained. On the other hand the difference in scattering power of 10 per cent required to produce a visible difference in contrast on a plate, is found to exist between a great variety of organic tissues and their surrounding media, so that the range of possible specimens is very wide, and can be artifically widened by the injection of heavier chemicals.

(*c*) The great depth of focus, as compared with the light microscope, also has advantages and disadvantages. It assists in the rapid exploration of specimens, since the whole of an object thin enough to be used as specimen will be in focus at the same time. But it correspondingly leads to the superposition of the detail of successive layers in the structure, where these exist, and makes high resolution difficult to attain in a specimen which is very much thicker than the resolution sought.

(*d*) The susceptibility of electrons to scattering demands that the whole beam path should be in vacuo. Specimens must therefore be dried and mounted before insertion in the microscope, a procedure which kills most living material. It is thus impossible to observe living material in the electron microscope by any of the techniques so far developed. This is, perhaps, its most serious disadvantage as compared with the optical microscope, especially when it is borne in mind that it was just the possibility of observing these details of cells and tissues which lie outside the resolution of the latter which made the electron microscope so interesting an invention to most biologists.

(*e*) Even if some means can be found of preserving living specimens within the electron microscope, it is still highly problematical how long they would withstand the intense ionising and heating effect of the electron bombardment. The intensity of beam required to produce good illumination at very high magnification is already such as to carbonise most specimens in a very short time. The interpretation of electron micrographs therefore needs very careful control, if effects produced by the beam are not to be ascribed to the original object itself. It is advisable to take a range of exposures at different beam currents and voltages, as well as different magnifications, and then to compare the results with those given by optical and ultra-violet microscopy, in order to ensure a true evaluation of the details recorded in the image.

All in all it will be seen that electron microscopy is at present beset with limitations both in choice of specimens and in interpretation of results. At the same time it must be remembered that, in comparison with the highly developed state of optical microscopy, it is still in its infancy as a research technique.

5. *Applications.*

(*a*) *Size and Shape of particles: smokes, dusts, bacteria, viruses.*

Smokes, dusts. The most straightforward use of the electron microscope is for determining the size and shape of particles which are "ultra-microscopic" in the ordinary sense of the term. They may be collected on a collodion membrane, a wire-gauze, glass fibres, or other supporting surface.

The technique has many applications in the paint, oil, and other industries where finely divided pigments and powders are employed, as well as in the study of smokes and war-gas dispersions (Plate 12). The examination of dusts caused in mines and industrial processes makes it of use in industrial health work, where many problems are concerned with particles smaller than one micron.

The particles must first be dispersed and the larger units removed, either by chemical means, by centrifuging or filtration. In the case of airborne particles the problem is rather easier. In either case the sample for examination is then collected on the specimen holder, for introduction into the electron microscope. The usual support is a film of collodion, of the order of 100A in thickness, prepared by evaporating a few drops of a 1 per cent solution of cellulose acetate or nitrate on the surface of water. Such films are at the same time sufficiently strong to withstand drying and heating in the electron beam, and yet structureless and thin enough to transmit the major part of the beam without appreciable scattering.

An extension of such particle size determinations is the recording of the physical changes accompanying chemical reactions involving small particles. Very little has yet been attempted in this very interesting field, but the Eastman-Kodak Laboratories have done some very interesting work on the mechanism of the photographic process in silver emulsions.

Bacteria. Most bacteria are already sufficiently visible in the optical microscope for considerable information to be obtained as to their size and shape. The electron microscope enables finer details to be investigated, such as the flagella (Plate 13), and something of the internal structure to be elucidated (Plate 14). It also can follow much more readily the changes which take place in natural reproduction or in artificial physical and chemical conditions.

The bacteria are either deposited on a supporting membrane from solution, as already described, or they may be transferred directly from a slide on which they may have been cultured to the holder. In this case a thin layer of collodion solution is painted over the culture, allowed to dry, and then stripped off, when the bacteria usually come off with it.

A great deal of survey work has already been done in this field (see Donovan, reference 4) but systematic studies, such as that of life cycles, are only now beginning. Many types of bacterium have been photographed (Plates 13 to 17) and some attempts made to observe the effect of bacteriophages on them (Plate 18). The action of antibodies and of penicillin have also been investigated, and the effect of X-rays in producing mutations.

Recent developments in methods of accentuating surface relief have enabled observations to be made on the structure of the surfaces of bacteria, as well as on their internal form (see Plate 15).

The major limitation in observing bacteria, however, is this necessity to dry and mount the specimen for insertion into the vacuum of the microscope. It is thus possible only to take a series of "snapshots" of different individuals at different stages in development, instead of observing the same bacterium throughout its history. This problem remains to be solved.

Viruses and Bacteriophages (or bacteria-destroyers) come next in the size scale after bacteria. Whilst bacteria are visible in the light microscope, the former show up only in the ultra-microscope, although their existence had also been inferred from biological and X-ray investigations. The electron microscope makes them fully visible, bringing direct confirmation of the results of other methods of examination. They are particularly interesting because they form an intermediate link between living and non-living matter, both in respect of size and in complexity of organisation.

The virus apparently can exist only in connection with "host," being parasitic on plant or animal matter. In general the plant viruses are smaller and simpler in constitution than the animal viruses, and some of them have been prepared in what seems to be pure crystalline form. The bacteriophages (or bacterial viruses) occupy an intermediate position. It has been suggested that the plant viruses, and probably the bacteriophages also, are really nucleo-proteins of high molecular weight, each individual being perhaps a single molecule.

X-ray diffraction methods showed that certain of the plant viruses, such as those causing tobacco and tomato mosaic disease, consist of rod-shaped particles about 3000A long and 150A in diameter. These conclusions have now been confirmed by electron microscopy, which shows us the separate particles (Plate 19). Successive micrographs show clearly the tendency of the particles to aggregate into threads and clusters, but there seems to be a minimum size below which smaller fragments are not observed ("molecules"). This makes the virus a useful means of magnification determination in electron microscopy (Plate 15).

The animal viruses are not only larger, but seem to have some internal structure. There has been some controversy over the size and shape of the influenza virus, which is readily visible in the electron microscope. It now seems to be established that the primary particles are spherical bodies of some 1,000A in diameter, but that curious connected growths exist along with them. Anderson has examined the vaccinia virus and shown them to be rectangular in shape, resembling a brick in form and containing five dense areas rather like the five spots of a die.

Considerable work has also been done on bacteriophages ("phages" for short), previously known only from centrifuge and filtration experiments. They are found to have an extremely constant and characteristic appearance within a given species, although different types may differ very much in size and shape. All have a roundish head and sperm-like tail, but the internal structure of the head differs considerably. Anderson showed that among different phages active on coli bacteria, the diameter of the head might vary from 500-1000 A and may sometimes be oval. The tails are sometimes well defined and sometimes faint, and occasionally missing altogether—although this may be due to disruption in drying and mounting. Luria and Anderson have taken series of micrographs showing the process of attack and lysis of a bacterium by bacteriophages; it appears that the latter are absorbed sometimes head-first and sometimes tail-first on the organism attacked.

Lepine (personal communication) has recently made an intensive investigation of the variation in size and shape of three types of phage, at the Institut Pasteur, comparing the electron microscope results with those obtained with other techniques (the centrifuge and ultra-filtration). He finds that, except in the case of the smallest type investigated ("Para-A"), all three methods agree well as to size of the virus particles. The electron microscope enables direct measurements to be made. They are about 600-700 A across, usually oval in shape, and have tails varying in length from 1400 to 2100 A with different types, but remarkably constant in width (40 A). The standardisation of size within a given type is quite remarkable, and, taken together with the fact that no "young" or "old" individuals can be identified, suggests that the phage particles are produced by some sort of "chemical factory" process within the organism attacked. No reproduction process has ever been observed outside the host, and it also appears certain that the introduction of a single phage particle into the latter can bring about its complete lysis. The phage may thus be a single large molecule, or group of molecules, which enter into the living processes of the host, distorting them in such a way as simultaneously to disrupt the organism whilst reproducing large numbers of phage particles: a form of destructive auto-catalytic reaction.

Work in this field of macro-molecular particles is only just getting under way. But enough will have been said to show how essential is the contribution of the electron microscope to the investigation of these border-line particles, lying between the realms of living and non-living matter, and through the investigation of which we are coming nearer to an understanding of the nature of the living process itself.

Molecules. The present limiting resolution of the electron microscope (10-15 A) corresponds to the size of a chemical molecule containing only some 100 to 300 atoms. Such molecules are, however, still much larger than those of ordinary chemical substances even of an organic nature, such as sugars, fats, waxes, etc. But they are smaller than those essential units of living matter, the molecules of proteins which we are beginning to be able to identify with some degree of certainty. Apart from the viruses, therefore, which may or may not be single molecules, it is perfectly feasible to "see" many of the larger molecules with the electron microscope. Ardenne first obtained plates showing individual molecules of haemocyanin, a colouring matter of animal blood corresponding to our own haemoglobin. They appear as spheres of about 200 A in diameter, roughly agreeing with the known molecular weight of 7 million. Molecules of the haemoglobin of a pond-snail are shown in Plate 22. Edestin (molecular weight 300,000) and other protein particles have also been photographed, and American workers have obtained minute dots in observations on synthetic resins and rubbers which may well be the individual molecules of the polymerised material.

It must be recognised, however, that in searching for minute individuals of this order of size, it becomes difficult to pick them out against the diffuse background of the supporting film and of the other biological material which usually accompanies them. There is also the fundamental difficulty that the degree of contrast becomes very small when an organic molecule is placed on a membrane such as collodion, the density of which is much the same. Only the presence of heavier atoms, such as the copper in haemocyanin, and the iron in haemoglobin, makes sufficient contrast in the image. There is a possible application here also for methods of specific staining (see below).

The observation of molecules of comparatively simple compounds must wait until the resolution of the instrument is reduced to the region of 5-8 A, which is theoretically just possible in the present lenses. Calculation shows that single atoms, at least of the heavier elements, should give sufficient contrast to be visible if and when corrected lenses allow a resolution of a few Angstrom units only.

(*b*) *Sectioned Specimens.*

Single cells, even the smallest, are still more than 1μ in size and hence too thick to be penetrated by the electron beam of the electron microscopes at present commercially available. It is thus not possible to observe the details of a whole cell at once on the object stage, even when dried in vacuo. A higher accelerating potential would give the beam sufficient penetrating power to get through the smaller cells, and the Philips experimental high-voltage instrument has been able to record micrographs of yeast cells at a voltage of 350 kV. Apart from this future development, the only means of investigating cell details is by sectioning and mounting layer by layer.

Sectioning technique is an important part of optical microscopy, but there is no need to cut a section smaller in thickness than the wave-length of light. So the best microtomes of the past were not made to cut sections thinner than 1μ, which is still too thick for the electron microscope. Recently attention has been turned to the design of super-microtomes, in which the cutting edge forms part of the circumference of a wheel rotating past the specimen at a speed of several thousand revolutions per minute. At such high cutting speeds it is now practicable to cut sections as thin as 0.1μ. Using such a "cyclonemicrotome," Fullam and Gessler have taken electron micrographs of sections of biological tissues, plastics, nylon, rubber, etc., to show the range of the method. Sjöstrand has described a much simpler method, using a micromanipulator under an optical microscope, by which even thinner sections may be cut. By this means it should be possible to investigate the detailed morphology of cells, including perhaps chromosome structures. An alternative method is that of "wedge-sectioning" first proposed and practised by Ardenne. In this, the specimen is embedded in a strengthening medium, the boundary set at an angle to the knife of a fine microtome, and a section then cut. The edge of the wedge will then be thinner than any whole section which could be cut, and may reveal features of interest. There remains, however, the considerable danger of damaging it in the process of removing the embedding material and mounting the wedge-section in the object holder. The investigation of the very fine-grain structure of cells is thus liable to be a difficult and hit-and-miss process, even with the electron microscope.

Staining. The development of methods of preferential staining may help appreciably in this direction, especially if higher operating voltages enable stouter sections to be employed. In light microscopy stains are of an optical nature, being dyes which are specifically taken up by some parts of a structure and not by others, thus making visible its details by selective absorption of light from the imaging beam. In electron microscopy such dyes are rarely of use, since they are organic substances of the same sort of density as the tissues to which they are attached, and hence produce no extra absorption or scattering of the electron beam. Here we require a "stain" to be of very different physical density from its surroundings, to make it effective in producing contrast in the electronic image. Marton first realised this, and experimented with osmium salts; others have since used phospho-tungstic acid, and gold and silver salts.

Remarkably successful use has now been made of such stains in the investigation of the structure of muscle fibrils, in which selective absorption of phosphotungstic acid is found to occur. In this way, also, the existence of a banded structure in connective tissue (collagen) fibres, unsuspected until the electron microscope was used, has been confirmed (Plate 23). There is a considerable field here for careful and painstaking investigation of specific effects, in much the same way as the technique of optical staining has been built up over a long period, mainly by empirical methods.

(*c*) *Surface Relief.*

The methods of electron microscopy so far discussed reveal internal features of material by a transmission process. Attempts have been made to construct reflection microscopes, but with only partial success. There are, however, two alternative means of making surface relief evident in the normal transmission electron microscope: that of preparing "transparent" replicas of the surface structure, and that of accentuating its contrast by depositing a beam of heavy metal atoms on it.

(*i*) *Replica Methods.* The simplest way of taking a replica of the surface of an object is to paint or flood a thin film of a plastic substance (dissolved in a volatile solvent) on to it. When the latter has evaporated, the plastic may be stripped off in the form of a thin film, which retains to a considerable degree the detailed convolutions of the surface.[1] Much work has been done on metal surfaces by this means, but little if any on biological material—probably on account of the difficulty of detaching the replica from the original surface in such cases.

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[1] A solution of Formvar in 1-4 dioxane is commonly used for the purpose, the fragments of film being then mounted in the specimen holder of the microscope in the usual way.

An alternative procedure is to employ a thermoplastic, such as polystyrene, to make a first replica under high temperature and pressure (160° C. and 100 atmospheres), and then to evaporate a thin film of silica to form a second replica upon the polystyrene surface. This method is highly successful with metal surfaces, which will stand the high temperature and pressure necessary in the first stage. The high mobility of the silica molecules when condensing yields an extremely sharp second replica. It is naturally inapplicable to biological material, but a recent variant of it employs a much lower pressure of 2 lb. per sq. in. only. Although a temperature of 150° C. is still required, Barnes, Burton and Scott show micrographs of red blood cells (Plate 24) and other biological material. Investigation of lower-softening thermoplastics may yet bring the method into greater use for biological purposes.

(*ii*) *Shadow-casting*. If a beam of heavy metal atoms is projected upon a surface at a small angle, it will be intercepted by any projections or other elevated features, which will collect an undue proportion of the deposit, whilst the areas immediately behind them will receive little or none. The physical density of the surface has been changed in such a way that, when used as a transmission object in an electron beam, the elevated portions will now pass none of the beam, whilst the neighbouring areas will be almost completely transparent: shadows will appear to be cast in the electron image which is formed. The method has thus been called "shadow-casting." Its effectiveness may be seen in Plates 13 and 15, where the surface relief of bacteria and their flagella are made clearly visible.

Wyckoff, who first invented the method, has used it to investigate not only the form of various viruses (compare Plates 19 and 20) but also the stages by which a virus "crystallises." He obtains remarkable evidence of the collective orientation of the beam mosaic virus particles into a cubic crystalline form, showing how it is built up layer by layer, the originally spherical virus particles suffering distortion in order to fit into the "lattice." He has also been able to demonstrate that the banded structure of muscle fibrils, mentioned above, is connected with a corrugated outer surface of the individual fibrils.

The shadowing method, which is usually carried out with a beam of gold atoms, promises to be of great use also in improving the contrast of very small molecules and other poorly scattering particles, near the resolving limit of the electron microscope. When contrast is sufficient, it can be usefully supplemented by stereophotography, two micrographs of the same object being taken with the object-holder slightly tilted in the second case. The elevations of the specimen can be determined by viewing the two stereophotographs in a special binocular frame, and employing the type of aerial contour-finder developed during the war for deducing ground relief from aerial photographs.

Conclusion.

It has only been possible to indicate in the short compass of this article the main methods of electron microscopy, and some of their present limitations. But it will be clear that it has already become a most useful supplement to optical microscopy, and promises to bring as great advances in the understanding of nature as did the original optical microscope in its day. We are at the beginning of new avenues of approach to the study of microstructures, and especially to those of living material. It is not even excluded that another decade or so of progress in the correction of electron lenses may allow us to locate directly the position of individual atoms in thin films. The major problem to be solved, otherwise, is that of the observation of living material in normal circumstances, instead of in the desiccated state.

FURTHER READING

For an elementary account of the subject, forming a useful introduction to this article, see E. M. Crook in Penguin Science News, 1, p. 128.

A fuller account of electron microscopy for the general reader will be found in:

V. E. Cosslett. The Electron Microscope. *Sigma Books.* 1947.

E. F. Burton and *W. H. Kohl.* The Electron Microscope. *Rheinhold Publishing Co., New York.* 1942.

For more advanced works, see the list of References below.

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Acknowledgments

The author expresses his thanks to all those who have kindly made prints available for illustrations, and who are mentioned individually in the captions ; also to the Director of the Paint Research Station, Teddington, by whose permission Plate 12 is reproduced, and to Prof. W. T. Astbury similarly for Plates 15 and 23; he is especially indebted to Dr. Lepine of the Institut Pasteur, Paris, for permission to include information communicated to the Electron Microscope Conference held in Oxford in September, 1946. All the prints reproduced were taken with the magnetic electron microscopes (with the exception of Plate 18, taken with the electrostatic microscope shown in Plate 9).

THE BIOLOGY OF SHIP FOULING

By K. A. Pyefinch

EVERYONE will be familiar with the dense masses of seaweeds which clothe the rocks of the sea shore between tide marks and with the heavy settlements of barnacles which completely cover intertidal rock surfaces in more exposed situations; familiar, too, are the masses of weed and associated animals thrown up on the shore after a storm. All these are clear evidence of the rich plant and animal life of the intertidal and sub-littoral zones of the sea shore. Settlement of plant spores or the larvae of sedentary animals is unfortunately not confined to the rocks and other surfaces between and below tide marks, but can occur on any suitable surface immersed in the sea. Ship's hulls can offer such suitable surfaces and the settlement of plants and animals on them creates a problem which affects, to a greater or a less extent, every shipowner. Heavily fouled ships carry over 100 tons of fouling and cases have been recorded where over 300 tons of plant and animal growth have had to be removed in dry-dock.[4]

Such spectacular cases of heavy fouling are rather the exception than the rule, but the settlement of smaller quantities of fouling has important effects. Perhaps the most direct effect is on speed, as the presence of fouling increases the frictional resistance to the movement of the ship through the water. Alternatively, if a given speed must be maintained if at all possible, this increased frictional resistance means an increase in fuel consumption.

It has been estimated[6] that the maximum speed of a battleship of 35,000 tons standard displacement, operating in temperate waters, will have been reduced by 1½ knots at the end of six months out of dry-dock or, to maintain a speed of 10 knots, the consumption of fuel must be increased some 45 per cent. The corresponding estimates for a destroyer (1,850 tons standard displacement) are a loss of maximum speed of 2 knots and an increase of fuel consumption of 50 per cent. Under tropical conditions, these estimates can be approximately doubled. These figures for naval vessels refer to peace-time conditions, when considerable periods are spent in port; the corresponding estimates for merchant ships, which spend a greater proportion of their time at sea, are rather less.

The steel hull of a ship is painted with two kinds of composition. First it receives two or more coats of an anti-corrosive or protective paint, which prevents corrosion of the hull—a bare steel hull would rapidly corrode in sea water—and, secondly, a coat of anti-fouling paint, which is applied over the anti-corrosive coats. The function of the anti-fouling coat is the prevention of fouling settlement. This paint contains poisons, often compounds of copper and mercury, which are released slowly when the composition is immersed. The rate of this release is important—if it is too great, poison will be wasted, if too small, settlement of fouling organisms will be possible. Since the amount of poison contained in the paint film initially is limited, it follows that an anti-fouling paint has a limited "life," as its poison content becomes exhausted, or the rate of poison release falls too low to prevent fouling settlement. In formulating an anti-fouling composition, the paint technologist therefore tries to design a paint which will allow the contained poison to be used most economically and so give the paint as long a life as possible.

Most anti-fouling paints seem to exert their action in the way just outlined; it is therefore necessary to dry-dock a ship periodically to allow this coating to be renewed. The cost of this renewal is a further item in the expenses due to fouling settlement.

Loss of propulsive efficiency and the cost of dry-docking, cleaning and re-painting are direct results of the settlement of marine organisms on exposed surfaces, but the indirect results of this settlement are almost equally important and costly. Loss of propulsive efficiency means slower voyages, more time spent at sea and higher running costs and may lead to the loss of markets or cargoes. Under war-time conditions, where maintenance of speed in convoy is of prime importance, a heavy fouling settlement is certainly dangerous and may be fatal. It is thus difficult, if not impossible, fully to assess the cost of fouling to the ship-owner, but it is clear that a solution of the fouling problem, and the provision of means of adequate protection from fouling settlement would be a substantial contribution to the economical working of our shipping.

It will be readily appreciated that the chances of fouling settlement are not equal in all waters and at all times of the year. Polar and temperate waters in general offer less chances of heavy fouling than tropical waters and fouling settlement is much more markedly seasonal in its occurrence in the former than in the latter. American workers[1] have divided the waters of the world into ten areas, each characterised by distinctive features of its fouling. These ten areas can be arranged in a series showing decreasing severity of fouling. Zones 1 and 2, which head the list as the regions where fouling is most severe, extend as a belt running roughly 30° north and south of the equator. They are followed by Zone 3, a small area off California. Less severe fouling incidence characterises the Mid-Atlantic region, which is Zone 4, and the Mediterranean and Black Sea, which are grouped together as Zone 5. Zone 6 is a small zone, including only the Baltic Sea. Less severe fouling still is a characteristic of the North Pacific and North Atlantic, which form Zones 7 and 8 respectively. Last in the list, with least severe fouling of all, appear the Antarctic and Arctic regions, which form Zones 9 and 10.

These global divisions are useful in indicating general areas of fouling severity, but it must not be assumed that fouling conditions are equally severe at all ports within one zone. Information is gradually accumulating about fouling conditions in the main ports of the world and it is becoming increasingly evident that many have individual characteristics, which are sometimes of a minor nature, but which may be of major importance in influencing fouling settlement. The fouling characteristics of *ports* are of particular importance since fouling organisms only settle when a ship is in port; no settlement takes place when at sea. More than this, the larvae of some fouling organisms can only settle, even in port, when the tidal flow is not too great. Recent work[3] has shown, for example, that water velocities of under 1 knot will prevent the settlement of the larvae of some of the important fouling barnacles.

Growth of the settled organism is possible both in port and at sea, but it seems likely that under the latter conditions growth rate is reduced. Recent American work[3] has shown that this is certainly true for some species of barnacles and it would seem likely to be true for other animal fouling forms. The great majority of these feed by filtering, by one means or another, smaller organisms from the water and it is difficult to see how the various filtering mechanisms involved could operate at their maximum efficiency at the water speeds produced by a ship in motion.

Many of the ports in temperate waters can be described as "clean" ports, that is, ports in which the chances of fouling are mainly slight. In contrast to these are the "dirty" ports of tropical and sub-tropical waters, where the chances of heavy fouling are much greater. Few fouling organisms can survive immersion in fresh water for extended periods so that freshwater ports (*e.g.*, Buenos Aires, the St. Lawrence ports) may have a cleaning effect if fouling is already present on a ship calling at such ports. Under such conditions marine organisms are killed and drop off, either before the ship leaves port or as soon as she puts to sea. If the fouling organisms present are mainly barnacles or tube-worms, such cleaning ports have little immediate effect as, although the barnacle or tube-worm is killed, the shell or tube remains and frictional resistance to movement is not much decreased.

If the hull is fouled with "shell" a type of cleaning port which can be much more effective is one in which the water contains much sand and suspended debris which, swept over the ship's surface by a strong current, can have a most potent scouring action. This can be sufficient to wear down shell fouling and after a stay in a scouring

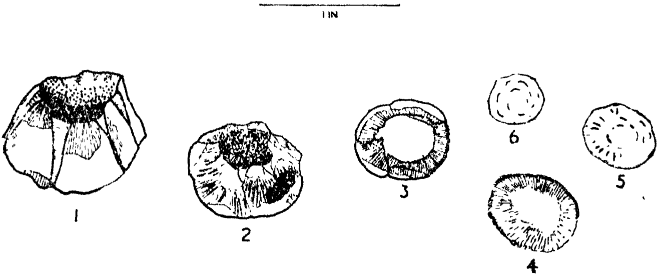

Fig. 1. *The Effects of a Scouring Port.* A sample of a population of barnacles removed from a ship which had spent three weeks at the Congo port of Matadi.

port a ship which entered fouled with barnacles and tubeworms may put to sea again completely free from these fouling forms. Such scouring ports, of which Calcutta and the Congo port of Matadi may be cited as examples, do not seem to be invariable in their action—much seems to depend on local conditions at the time of call—but at its maximum their action can be most effective. Figure 1 illustrates the effect of a three-week stay at Matadi on a barnacle settlement. Barnacles over half an inch in basal diameter have been reduced to their calcareous bases (5, 6) and erosion is apparent even on the larger shells (1-4).

The incidence of fouling settlement is thus dependent upon a number of factors. It may perhaps be helpful to list some of the more important factors which seem to be concerned—this list does not pretend to be complete but it gives some idea of the main factors which are important.

(*a*) *Factors Favouring Fouling Settlement and Persistence.*

(i) A long interval since the last dry-docking. If the period of effective "life" of the anti-fouling composition has been exceeded, there is nothing to prevent settlement taking place.

(ii) A route chiefly in tropical waters. Large numbers of settling stages are available the year round in such waters and any inadequacy in the anti-fouling coating will result in heavy fouling.

(iii) Long stays in port. A lengthy stay allows fouling organisms to become well established before being exposed to the more rigorous environment of rapid movement through the water. Further, the longer the time spent in port, the greater are the chances of settlement.

(iv) No calls at freshwater or scouring ports, *i.e.*, no chances of loss of fouling which may have settled earlier in the voyage.

(v) Short voyages between ports. A lengthy sea passage undoubtedly can kill fouling forms, especially if settlement has occurred only shortly before the ship leaves port.

(*b*) *Factors Adverse to Fouling Settlement and Persistence.*

(i) A short interval since the last dry-docking.

(ii) A route confined to polar or temperate waters.

(iii) Short stays in port.

(iv) Calls at freshwater or scouring ports. The longer the stay in such ports, the more effective their action.

(v) Long sea passages between ports.

Thus the fouling problem may not be acute for the shipowner maintaining coastal vessels in temperate waters, since his ships, though frequently in port, are rarely there for any length of time and frequently berth in fresh or estuarine water. For example, in the course of a service period of 152 days a small coaster (roughly 1,000 tons gross) made roughly 30 calls, with an average period in port of 3½ days and entered fresh or estuarine waters on at least eight occasions during the trip. When dry-docked, fouling settlement was negligible.

Fouling settlement may also not be serious on the fast passenger liner, with her long sea passages and comparatively short periods in port, but for the cargo vessel making lengthy stays in tropical ports, the situation is very different. Here lengthy exposure to severe fouling conditions may be intensified by a series of short sea passages as a series of cargoes are discharged or loaded.

Absence of fouling settlement on the hull when dry-docked is thus by no means an unqualified tribute to the efficiency of the anti-fouling composition used; a number of other reasons may account for this result.

A full and accurate interpretation of the fouling present on a ship's hull therefore demands the possession of a good deal of information about the way in which the interval since the last dry-docking has been spent. In particular it is necessary to know the sequence of ports visited and the length of time spent in each port. With this information it is sometimes possible to build up what may be termed a "fouling history" of the voyage. In its most complete form such a history would give a full account of the sequence of fouling settlements which have been encountered during the course of the voyage and would afford a clear indication of the period over which the anti-fouling coating had remained effective. Full interpretations of this kind are a matter for the future, because their preparation depends upon knowledge not yet available or accessible. Yet even with the limited amount of knowledge at present available a good deal can be deduced from a sample of fouling. Measurements of the "shell" may reveal the presence of several settlements, a detailed examination of the sample may show the superposition of a settlement of one organism over a previous settlement of another, or the presence of dead "shell" may be correlated with a lengthy call at a freshwater port at one stage of the voyage. From such indications it is often possible to make shrewd guesses about the general sequence of settlement and something of a fouling history can be constructed. Much more information is needed before such guesses can become reliable deductions. A clear idea of the biological and other characteristics of each port of call is perhaps the first necessity, but this must be supplemented by knowledge of the growth rates and survival of the major fouling forms under a variety of environmental conditions—when the ship is at rest or in motion, in warmer and in colder waters, in marine or estuarine conditions, etc. The fouling history will then be an important means of assessing the efficiency of the performance of an anti-fouling coating under service conditions.

The fouling forms which settle on ships can be broadly classified into plant and animal forms, and this distinction is often immediately obvious when a ship is inspected in dry-dock. Plant settlement is usually limited to a narrow belt at the water line, whereas animal fouling, though it may extend up into this belt, is more usually confined to the sides below the plant belt and to the bottom flats of the hull below the bilge keels.

A considerable number of plant and animal species have been recorded from ships' hulls—one comprehensive survey[4] lists some 16 species of seaweeds and 66 species of animals—but the great majority of these do not occur at all commonly and thus are of little practical importance. Analysis of the fouling organisms present on ships dry-docking in this country indicates that surprisingly few plant and animal species are represented at all commonly. The most common forms are briefly described below.

The green alga, *Enteromorpha*, is the most common plant fouling form and its long, grass-like, green filaments are an almost universal component of water-line fouling. Under favourable conditions its growth rate is rapid, so that strands several inches long are by no means uncommon. The branched filamentous brown alga *Ectocarpus* is sometimes found associated with *Enteromorpha.*

Among animal fouling forms, acorn barnacles and tube-worms are the most important types. The acorn barnacles which settle on ships are mostly species of the genus *Balanus*—in temperate waters *Balanus crenatus* is a common form, whereas in tropical and sub-tropical waters *B. amphitrite* and *B. tintinnabulum* occur most frequently. All three species closely resemble *B. balanoides*, the common acorn barnacle of the shore, in their general appearance.

Barnacle fouling is particularly severe in certain areas, of which the West African coast may be cited as a good example. A recent analysis of fouling samples from ships calling at ports on this coast indicates that roughly 90 per cent had barnacle fouling.

The sinuous calcareous tubes of species of the genus *Hydroides* are frequently conspicuous features of bottom fouling, and this tube-worm almost ranks with barnacles in importance. Unless they are growing in crowded conditions or in still water, the calcareous tubes made by this worm are attached to the substratum for the whole of their length, and this characteristic is one which particularly favours their persistence on a moving surface. Tube-worm fouling is frequently not confined to the hull but also extends on to the bosses and even some way up the blades of the propellers.

The delicate stolons and stems of hydroid Coelenterates (*e.g.*, *Obelia*, *Tubularia*) are also common constituents of the bottom fouling, but, because of their delicacy and fragility, their importance from the practical aspect of increasing resistance to motion is far less than that of barnacles and tube-worms.

Other animal forms which occur with some frequency are Polyzoa, colonial animals some of which form erect, branched growths, others produce flat encrusting growths which spread over the substratum and which can grow over their sedentary neighbours. Stalked barnacles (*Lepas* spp.) also occur occasionally, oysters are moderately common, and sometimes heavy settlements of mussels and sea-squirts (*Ascidians*) occur. None of these forms are as common as acorn barnacles or tube-worms and many of them are found only when fouling settlement has been heavy and a dense intermingled mass of animal fouling forms of all kinds is present

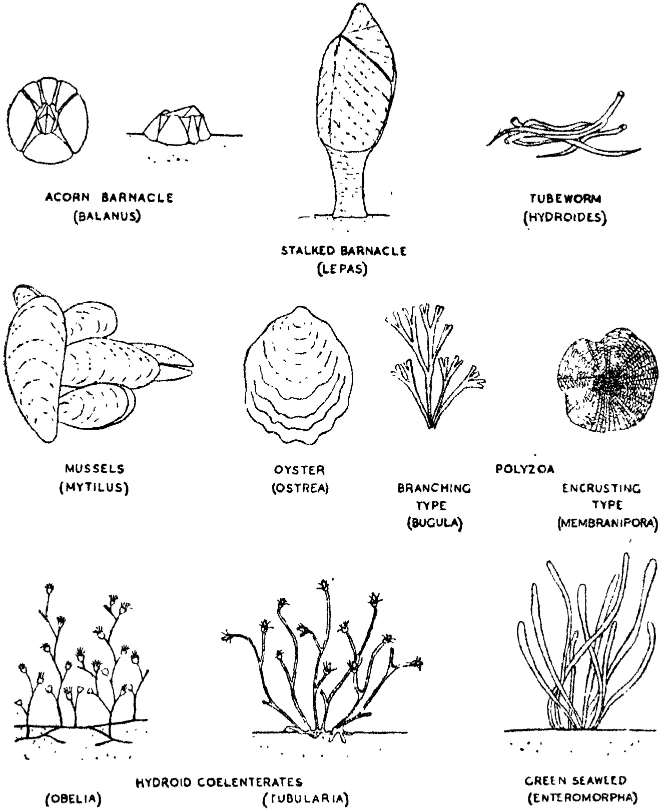

Fig. 2. *Common Fouling Organisms.* Approximately half natural size, except Obelia, which is about four times natural size. These figures have been drawn from typical samples of fouling, but the sizes shown do not necessarily indicate the maximum size which can be attained on the hull of a ship.

Figure 2 shows line drawings of the most common forms mentioned in this section.

This brief description of the main members of the fouling community that may occur on the hull of a ship takes little account of their inter-relationships or ecology. These inter-relationships are not easy to discover, as observations are necessarily limited to an inspection at the end of the run. That it has been possible to construct tentative fouling histories for some voyages indicates that it is possible to deduce something of these inter-relationships in favourable instances, but much detail is missing which could be added if inspections could be made during the course of the voyage.

Fortunately it is possible to obtain a much clearer picture of fouling settlement and of the ecology of fouling organisms from observations made on experimental anti-fouling compositions under test. Such tests are usually carried out on suitable surfaces immersed in the sea from a raft or pontoon moored offshore. The painted surface is thus continuously immersed at a depth which remains approximately constant and which, by altering the method of suspension or attachment of the painted panel to the raft structure, can be varied as desired. Such exposures can be inspected as frequently as necessary and the sequence of settlements which may occur followed in some detail.

The factors affecting settlement on painted surfaces exposed from a raft differ, to some extent, from those obtaining on the hull of a ship. The raft is usually stationary, so that organisms which settle on surfaces suspended from it are exposed only to the moderate water velocities of the tidal flow—the ship is, so to speak, always in port. This has an effect in that some members of the fouling community are much more conspicuous on raft-exposed surfaces than they are on ships. This seems to apply particularly to hydroid Coelenterates such as *Obelia*. On raft-exposed surfaces the delicate stems of this hydroid can withstand the relatively low water velocities to which they are exposed, but there is evidence which suggests that these stems are broken away when a ship is under way, leaving behind only the branched attachment threads which are closely applied to the surface for the whole of their length. *Obelia* is thus a conspicuous member of the raft-fouling community, but far less conspicuous on a ship.

As rafts are usually moored not far from the shore, the chances of local infection, by spores or larvae liberated from plants or sedentary animals on the shore near-by, are high. This effect is increased by fouling on the raft itself, if the latter—as is sometimes the case—is painted with an ineffective anti-fouling composition, or is not painted. The effect of this factor rather depends upon the type of life history of the fouling organism concerned. Organisms which have free-swimming larvae with a long larval life (*e.g.*, barnacles, tube-worms) occur equally commonly on raft-exposed surfaces and on ships. During their free-swimming period, these larvae must be carried considerable distances from their parents, so that the presence of the latter in the immediate neighbourhood of the exposed surface is not essential. Organisms which produce larvae with a short larval life present a different case. Local sources of infection become important and marked differences may be found in their colonisation of raft-exposed surfaces and of ships. The hydroid *Tubularia* would seem to be an example of this. This hydroid produces a larva which settles, very shortly after liberation, in the immediate neighbourhood of the parent form. *Tubularia* can occur very abundantly on raft-exposed surfaces but it is a minor component of ship fouling.

The existence of these two factors means that a raft test can be more stringent than a test of the same composition applied to the hull of a ship. Raft exposures are therefore a particularly useful means of detecting whether an anti-fouling composition possesses adequate anti-fouling properties or not. As a test of the length of time for which these anti-fouling properties can be maintained, a raft exposure is less useful. Mention has been made earlier of the loss of poison from the surface of an anti-fouling paint. The rate of this loss is increased if the surface is moving through the water at the speed of a moving ship. The length of life of an anti-fouling composition, estimated only from raft tests, is therefore too long as the rate of loss of poison, though adequate to prevent fouling settlement, is not directly comparable with the rate of loss from the same composition on the surface of a ship.

Settlement of fouling on a raft-exposed surface is governed by two major factors, the seasonal factor and what may be termed the sensitivity factor. In other words, settlement is governed by the availability of settling stages and by the ability of these stages to settle.

In tropical waters breeding, and therefore settlement, of some sedentary forms goes on throughout the year. Thus studies made in Madras Harbour[2] show that the tube-worm *Hydroides norvegica* and the acorn barnacle, *Balanus amphitrite*, both important fouling forms, continue to breed the year round; settlement of barnacles can take place at any time of the year in the West African port of Lagos, and so on. In temperate waters, however, the situation is rather different. Here most fouling organisms have restricted breeding seasons and their settlement is therefore very definitely seasonal in its occurrence. Figure 3 shows the settlement periods for a number of fouling forms. From this figure it is clear that diatoms alone occur throughout the year, other plants and animals have restricted periods of settlement—usually confined to the summer months.

A surface immersed from November to March will not become heavily fouled by any of the forms listed and

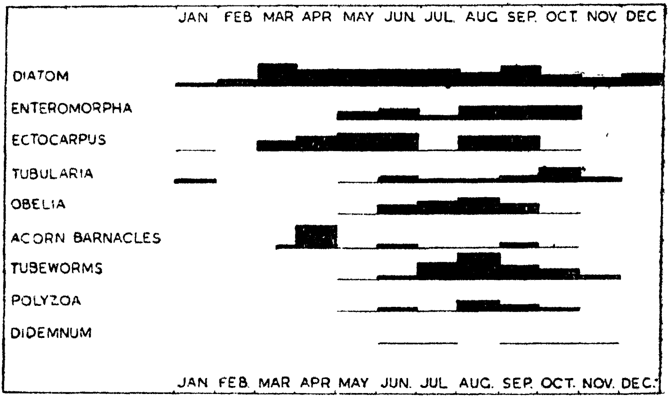

Fig. 3. Seasonal settlement at Millport, Firth of Clyde, 1945.

settlement at other times of the year depends largely upon the time of year at which exposure is made. Thus a surface exposed in April will become colonised by acorn barnacles, one exposed in June by *Enteromorpha, Ectocarpus* and *Obelia,* whereas tube-worms, the hydroid *Tubularia* and possibly the colonial Ascidian *Didemnum* will be present on exposures made later in the summer. This figure has been drawn from data obtained at Millport, Firth of Clyde. At other points round our coasts the details of this picture of seasonal settlement differ slightly. Variation in detail also occurs at one site from one year to another—the general sequence of settling forms remains the same, but marked fluctuations in the abundance of particular organisms can occur. For example, acorn barnacle settlements vary markedly in their abundance from year to year. At Millport in 1943 settlement of *Balanus balanoides* was light, in 1944 it was heavy, in 1945 moderately heavy (see

Figure 3) but in 1946 settlement of this species of barnacle has been very light.

These variations in the seasonal incidence of fouling forms in temperate waters mean that a constant check must be kept on the general seasonal changes going on, otherwise estimates of the anti-fouling performance of raft exposures may be misleading and inaccurate.

Sensitivity of the settling stage is a factor which is at least equally important with the seasonal factor in controlling colonisation of the surface of an anti-fouling composition. The rate of release of poison from such a composition varies with the time that the composition has been immersed. The actual pattern of this variation may vary with the particular type of formulation employed, but in many cases the rate of release is initially high and later decreases. There is reason to suppose that, immediately over the surface of the paint, there is a layer of water which, if the paint is exerting an adequate anti-fouling action, contains an appreciable concentration of poison. The actual thickness of this layer is not certainly known, but it seems likely that the settling stages of many fouling organisms are small enough to be contained wholly within it. If successful settlement is to be achieved, therefore, the settling stage must be able to withstand whatever concentration of poison there is present immediately over the surface of the paint.

Fouling organisms vary considerably in their sensitivity to the poisons released from an anti-fouling composition so that, as the rate of release of poisons from the paint falls and the concentration of poison immediately above the surface of the paint decreases, settlement of a wider and wider range of organisms becomes possible. The list below gives a rough idea of the order of sensitivity of the chief fouling organisms and expresses, assuming ideal conditions in other respects (*e.g.*, the availability of the appropriate settling stages), the order of their appearance upon an anti-fouling composition immersed in the sea.

Least Sensitive	Bacteria
	Some Diatoms (e.g., *Amphiprora*, *Achnanthes*, *Schizonema*)
	....
	Tubularia
	Ectocarpus
	Barnacles
	Obelia
Most Sensitive	Tube-worms, Mussels, encrusting Polyzoa, the larger brown sea weeds (e.g., *Laminaria*), some green sea weeds (e.g., *Ulva*), etc.

Some marine bacteria are very insensitive to the poisons commonly used in anti-fouling paints, *e.g.*, copper, and the appearance of a film of slime which is bacterial in origin is often the first settlement to appear on the paint surface. The difference in sensitivity between these bacteria and the diatoms which are the next members of the sequence is probably considerable, but the latter can settle on a paint surface which is releasing poison at a considerable rate. *Amphiprora* forms a slime, within which the cells of the diatom lie closely packed. *Achnanthes* is a stalked form and a heavy settlement of this diatom has a characteristic furry appearance, like that of a carpet with a fine, closely-set pile. *Schizonema* can form upright, branched growths, which are just visible to the naked eye and which consist of branched mucous tubes, within which the cells of the diatom are packed.

It is most unlikely that any of the settlements so far described have any appreciable effect on the resistance to the movement of a surface on which they have settled through the water. As fouling organisms in the practical sense these can therefore be neglected, and it is usual to rate any paint surface bearing only bacterial slime or these diatom growths as unfouled. In the next member of the sequence, however, the hydroid *Tubularia,* the first fouling organism which forms "macroscopic" fouling is encountered. In the sequence above the broken line therefore indicates the boundary between an "unfouled" and a "fouled" surface. It is the aim of the paint chemist to produce a paint which will prevent the settlement of *Tubularia* and of all the organisms which appear below it in the fouling sequence. Settlement of diatom is neglected, in fact, the persistence of this type of fouling may be taken as an encouraging sign, in that it indicates that the rate of release of poison is *just* high enough to prevent settlement of macroscopic forms, *i.e.*, the poison contained in the paint is not being wasted by being released at too great a rate.

Ectocarpus, acorn barnacles and the hydroid *Obelia* can settle on surfaces which have progressively lower rates of release of poisons, that is, on surfaces which are becoming less and less effective. The final group of organisms is that of forms which are very sensitive to poisons and their appearance on a paint means that its anti-fouling properties are negligible.

This sequence of possible settlements should not be regarded as an example of succession, in the sense that this term is usually employed in ecological studies. There is little evidence that the settlement of one form is dependent upon that of a predecessor; this sequence is controlled by an artificial environmental factor—the rate of release of poison from the surface on which settlement is taking place.

Though these two factors, that of sensitivity and that of season, seem to be of fundamental importance in affecting settlement, it is necessary to carry this story one stage further. As successive settlements occur, or as the members of an earlier settlement grow and spread over the surface, the chances of later settlements alter, even though settling stages are available and the rate of release of poison is low enough to allow their settlement. The persistence of an earlier settlement has an important effect on the later history of the surface. Thus, a heavy settlement of barnacles will soon come to cover the surface with a solid sheet of these organisms, so that no space is available for later settlements. Other settlements are more transient in their importance, *e.g.*, the hydroid *Obelia* flourishes in mid-summer, but dies down after a few weeks of exuberant growth, leaving only the delicate tracery of its attachment threads on the paint surface, which have little effect on the possibilities of later settlements. Rapid growth of one organism may smother and kill earlier settlements and so present a final picture of colonisation which misrepresents the sequence that has actually occurred. It would be tedious to enter into greater detail, since almost every exposure presents a problem in itself, but, in an attempt to give some idea of the appearance of paint surfaces at different "stages" of fouling, sketches have been drawn of the fouling present on a series of surfaces. These are shown in Figure 4. In this figure, patches A and B represent surfaces which would be rated as "unfouled," patch C a surface which has become fouled with a number of moderately resistant forms, and patch D, with its heavy settlement of a variety of forms—including those known to be most sensitive—a surface which can be regarded as devoid of anti-fouling properties.

This brief account of the factors which seem to control settlement on a painted surface exposed from a raft indicate something of the complexity of this problem in applied ecology. It emphasises the true complexity of ship fouling, a complexity increased by the obscuring or elimination of important stages in the sequence of colonisation.

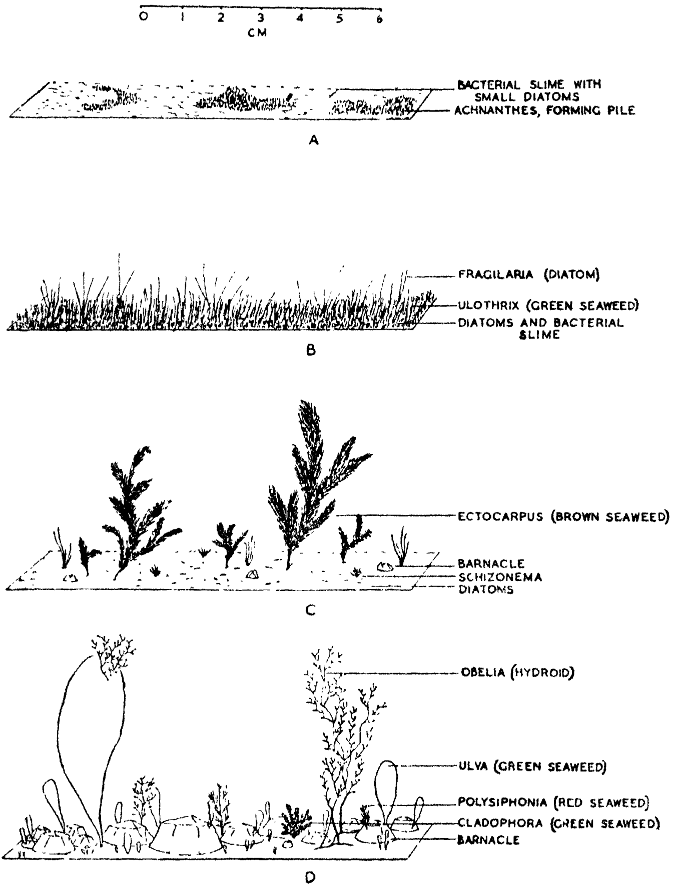

Fig. 4. Types of community on paint surfaces.

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BEASTS OF BURDEN

By Alec Parker

BEASTS of burden, using the term to include animals used for draught, carrying loads, and riding, are confined to one group of the animal kingdom. This is the mammals. When we enquire into the features of structure and behaviour which befit an animal for work of this type, this does not seem surprising. For one thing, mammals are preeminently the largest forms of land life of the present day, and large size, though not necessarily accompanied by great strength, is clearly essential for its development. (There was a time, of course, when the largest land animals were reptiles, but their regime ended long before the appearance of anything resembling man). But strength alone is not enough. It would be of little use unless supplemented by amenability to handling. Here again mammals are at an advantage in being a group characterised by great plasticity of behaviour. Certainly in most, and perhaps in all cases where an animal becomes at all intimately associated with man, the demands made upon its capacity for modifying its natural behaviour must be considerable. When it is further expected to haul or carry loads—a state of affairs, one would think, quite unlike anything it would experience in the wild state—these demands must be intensified.

Not only are beasts of burden confined to mammals, but with two exceptions—the dog and the elephant—to hoofed mammals. This again is understandable. Taking the size range, for instance, we find that among land mammals the size of some of the hoofed members is exceeded only by the elephant, and approached only by large carnivores such as the tiger, the lion, and some of the bears. Coupled with this is the fact that the hoof is part of a limb which is particularly well adapted for running. Hoofed mammals are customarily divided into two orders. In one of these, the Artiodactyla—a large order including cattle, sheep, goats, swine, deer, antelopes, the camel and the llama—the hoof is cloven. In the other, the Perissodactyla—an order including the horse, the ass and the zebra—it is undivided. The latter type of hoof represents a single enlarged digit (that is, finger or toe), the others being either absent, or reduced to small and usually functionless splints. The cloven hoof represents two such enlarged digits. This condition is quite unlike the normal situation in mammals, where there are generally five digits of approximately equal size. Another unusual feature of hoofed mammals is that they walk on "tiptoe." Instead of the whole, or almost the whole, length of each digit touching the ground, as it does in most mammals, the only part to make contact is the tip. The result of this is that the entire weight of the body is borne by the one or two remaining well developed digits. To meet this strain the latter have become thicker, and consequently stronger, and their tips modified into the hard flattened surface which we term the hoof. On purely mechanical grounds we should expect an undivided hoof to be more capable of withstanding a thrust than one split along its midline, and the horse's capacity for pulling or carrying greater loads than can an ox of comparable bulk may, to some extent, be due to this.

Hoofed mammals are essentially herbivores, usually of the grazing type, and the unaggressive type of behaviour which we associate with this mode of life might be expected to be related to the amenability to domestication which the group displays. This supposition is open to doubt. The dog, perhaps the most completely tamed of all animals, for instance, is a carnivore. Herbivores like the rhinoceros and African buffalo, on the other hand, surpass any carnivore in their ferocity. With conspicuous exceptions like these, such generalisations can be of little value.

Of beasts of burden other than those with hooves, the elephant is of value mainly because of its great size and strength. Clearly, however, its behaviour reactions are also important. Indeed, when we reflect that the highly trained animals to be seen in India, for instance, are mostly captured from the wild state at a quite advanced age and trained subsequently, we are forced to conclude that its tractability is, in fact, remarkable.

The position occupied by the dog is rather singular, and though it is used for various purposes, of which that as an accessory in hunting is probably the most important, it is very likely that its widespread domestication is mainly a result of the extraordinary readiness with which it will associate with man. Opinion is now predominantly in favour of the wolf as the ancestor of all domestic breeds of dog, and many well authenticated cases testify that men can tame wolves. Since the oft recounted tales of children being reared by wolves seem, in some instances, to be founded on fact, the converse would also appear to be true. The tractability of the dog is rather curious, particularly since its exaggerated submissiveness to its master is in contrast to the general behaviour pattern of the carnivore group to which it belongs. The cat, also a carnivore, and again widely domesticated, rarely, if ever, reaches a comparable level of dependence. Perhaps a study of the behaviour of the wolf under natural conditions would provide an answer. It is conspicuous for its association in packs, and in such a social group responses such as those connected with submission to the leader might be expected to develop. Reactions of this sort, if they exist, might well be important in predisposing the animal for association with man.

Our chief concern, however, is with the dog as a beast of burden. For this purpose, obviously, its use is limited by its small size. Nevertheless, it is occasionally used in various parts of the world for carrying small packs, and on the continent it is still to be seen pulling the bread or milk cart. In England, presumably owing to the prevalence of zoophilic organisations such as the R.S.P.C.A., such practices are illegalised. Up to the time of the Spanish conquest of the New World, the dog was the only domesticated mammal possessed by the natives of North America. It is therefore not surprising to find that they have exploited it in more ways than one. Among these are its uses as a drawer of the sleigh, and of the "travois." The latter consists of two poles, one end of each of which is lashed to the animal, the other being allowed to trail along the ground. The baggage is tied between the two. Needless to say, such a method of transport is only feasible when the ground is fairly flat. The special peculiarities of the dog only become of real advantage in snow-covered regions. Here, its small size and light weight mean that it has much less tendency to sink in than a larger animal, while the readiness with which at any rate some types will work in teams, means that its slight individual strength is no obstacle to its being used to drag heavily loaded sleighs in unison with other dogs.

The most widely used type of sleigh dog is the huskie, employed mainly by Eskimos. A sleigh team of the Eskimo type consists of five or six dogs, each of which is attached to the sleigh by a single trace. The dogs spread out fanwise over the snow, so distributing the total weight over a considerable area. In the wooded country in which sleigh teams are employed by the North American Indians, the narrowness of the track frequently makes this method of attachment impracticable, and so the dogs are harnessed in file. A sleigh team is very much more than just a few arbitrarily chosen dogs. It has a definite social organisation, and when dogs unfamiliar with each other are harnessed to the same sleigh they are said to be almost uncontrollable. In a properly developed team the strongest animal holds an undisputed position as leader, and runs a little ahead of the rest. Nor is his social superiority confined to the trail, for a similar appearance of subservience is exhibited by the lesser members of the team over other matters, such as the portioning out of the food. In view of the fact that the huskie is probably very closely related to the wolf—it howls like a wolf, for instance, instead of barking like other dogs—a study of the similarity between the social organisation of the sleigh team, and that of the wolf pack, might be very enlightening.

In the Old World the place of the dog as a drawer of sleighs is taken by the reindeer. In some countries—Lapland for example—the use of the latter for this purpose is very common. Certain features of the reindeer make it more suitable for sleigh drawing than the dog. It can, for instance, negotiate rougher country. Being a herbivore, its feeding presents less of a problem, and wherever the snow is sufficiently thin it will feed itself by grazing. Dogs, on the other hand, require loads of meat to be taken along with them for food. The drawback of the reindeer lies in its greater weight, and consequently greater tendency to sink into the snow. It is, however, only just to mention that this is mitigated by the fact that the hoof is spread out to an unusual degree, so making for a wider dispersion of the pressure than would otherwise be the case.

As a beast of burden the reindeer is used not only for drawing sleighs, but also for carrying packs, and, in some parts of Siberia, for riding. Since the back of the animal is not sufficiently strong to bear the weight of a grown man, a reindeer rider sits well forward on the shoulders. The place of the reindeer in human economy, however, does not depend solely upon its provision of locomotive power. Among other things it is an important source of meat and milk, both in the Old World and in North America. North America has its own species of reindeer in the caribou, and in view of this it is rather surprising, at first sight, to find that all those domesticated there are of the Old World type. The explanation is that when, just over fifty years ago, it was proposed to introduce reindeer breeding as an industry in North America, it was felt that it would be quicker to import the already domesticated Old World reindeer than to attempt to domesticate the hitherto untamed caribou. The experiment proved successful, and so the latter has remained a wild species. There is no reason to suppose, however, that it must necessarily continue to be so indefinitely.

Specific as the reindeer is to Northern regions, a much more conspicuous example of suitability to a particular habitat among the animals exploited by man is the camel. The utility of this animal in regions of sandy desert is quite unrivalled. Its flattened and leathery soles enable it to travel over soft sand in which most hoofed animals would make little progress. It has special growths of hair situated at critical points like the entrance to the nostrils, which serve to protect the tender parts from particles of flying grit. It is not injured by the extremes of heat and cold to which desert regions are daily subject. And there is its well known capacity for enduring thirst. When conditions are at their most arid the camel will tolerate up to three or four days without water, while when it has access to the fresh spring pastures it will endure deprivation for a month without appearing any the worse. Its tolerance of food shortage is also exceptional, and is due to the hump. This is a store of fatty tissue, the size of which gradually diminishes as food is withheld. Since the oxidation of fat involves the liberation of a relatively large amount of water, its utilisation as a source of food by the camel may have an important connection with the thirst endurance of this animal.

Camels are divided into two species; the one-humped or dromedary, and the two-humped or Bactrian camel. As with horses these are subdivided into different breeds, some of which are suited for carrying heavy loads, and some for riding. The former may carry a burden of up to half a ton, though half that is more usual. The riding types travel faster, but are greatly inferior in strength. Important differences also exist between the two species. The Bactrian camel is suited to a more northerly climate than the dromedary, and is the type usually kept in Central Asia. Here, at one time, it was almost the only means of long-distance transport, and caravans of pack camels are still occasionally to be seen crossing the steppes of these desolate regions. It is also frequently employed in various agricultural operations, such as drawing the plough. The dromedary is more suited to the sands of North Africa and Arabia. It is the most useful domestic animal the Arabs possess, and to tribes like the Bedouin constitutes almost their entire livelihood. For them it provides not only its muscular energy, but milk and hides. The first, however, remains its most important contribution to human economy.

But what of the disadvantages of the camel? One is that its soft pads are too tender for rocky ground. Some attempt is sometimes made to circumvent this by sewing leather pads on to the soles, but obviously such measures cannot be really adequate. A more outstanding defect lies in its behaviour. On occasion, for instance, it will lie down, moving again only after the severest provocation. Even more annoying is its tendency to wander away from the herd when turned out at night to graze. Frequently it fails to return, so necessitating a long and perhaps unsuccessful search.

The elephant is estimated to be able to pull or push with a force approximately equal to that of fifty men. As we saw earlier, however, its value lies not only in its great strength, but also in its amenability to training. The readiness with which it can be taught to respond to words of command is well known. At the same time, the fact that it hardly ever breeds in captivity means that there can be no question of selective breeding having contributed to its tractability.

There are two living species of elephant, the Asiatic and the African. Of these, the Asiatic has long been tamed in India, where it is employed mainly for heavy work such as forest clearing. Its imposing size is frequently utilised in ceremonial parades in the same country, and it is also widely used by shooting parties. Its popularity with the latter is presumably to be attributed to the confidence which its size and solidarity inspires in those perched on its back. It is often supposed that the African elephant is less tameable than the Asiatic, but the tractability of the former has been definitely established within recent years by a successful attempt to use it for draught purposes in the Belgian Congo. Here it has been harnessed to the plough, and for these purposes is said to be distinctly more economical than mechanical tractors. Being a native of the country, it is relatively unaffected by certain diseases carried by the tsetse fly, which are responsible for such extensive loss among some of the domestic animals introduced from other regions. In all likelihood the African elephant was also used in ancient times. The Romans and Carthaginians used elephants in battle to break the ranks of the enemy—a foretaste of the armoured tank—and probably these were of the African type. Those employed by Hannibal in his famous march across the Alps furnish the most familiar instance of their use during these early historic times.

To-day, apart from its very limited utilisation in zoos and circuses, the elephant is not employed outside the tropics. Although the climatic range which it will tolerate is much wider than this, its use in temperate regions was always either as a show-piece or as a mobile battering ram, and in such parts its employment for other purposes, such as in agriculture, has probably never been very economical. It needs, for example, a large amount of food, and this, except in tropical regions where plenty of lush vegetation is available, must be difficult to find.

Though they are to be found on opposite sides of the globe, the yak and the llama have in common their inability to thrive except at high altitudes. The former inhabits the mountains of Tibet; the latter those of South America. With their similarity of habitat we should expect to find them sharing certain features which are adaptations to life in the mountains: their surefootedness, and development of an exceptionally thick coat of hair, furnish examples of these.

The llama was the only hoofed mammal to be found in South America in prehistoric times, and was of great importance in the economy of the ancient Inca civilisation of Peru. So dependent were these people upon it that the extent of their territory appears to have been determined largely by its distribution. Apart from a creature ancestral to, and resembling, the guinea pig, it was their only domesticated animal, and served not only as a pack animal but as a source of meat, hides, and wool. At present there are four types of llama. Two of them—the guanaco and the vicuña—are to be found only in the wild state. The other two—the llama proper and the alpaca—are domesticated. It is commonly supposed that the domesticated types are descended from the guanaco, but there is no decisive evidence for this. The alpaca is smaller than the llama, and is kept mainly for its wool. The llama itself is used mainly as a pack animal, and for this type of work it has many points in its favour. It is a close relative of the camel, for instance, and will go without water for several days. Its diet presents no problem, as it will usually feed itself on the herbage growing by the wayside. Furthermore, if not an animal with a pronounced capacity for learning, it is at least fairly docile. Its habit of spitting cannot be regarded as more than an annoyance. On top of these there are the adaptations to mountain life mentioned above. Yet in spite of these desirable features, the importance of the llama as a pack animal has greatly diminished. This is largely an effect of the introduction of the mule, and its relatives, the horse and the donkey. These animals are almost or quite as sure-footed, and can carry heavier loads. Consequently, it is only in the higher altitudes, where the special physiological make-up of the llama puts it at an advantage, that it still holds its own.

In the high mountainous regions of Tibet, the yak is still quite indispensable. Not only is it the only possible means of transport in many parts, but it is an important provider of meat and milk. Its maintenance, however, is no easy matter, since, although it will feed on coarse scrub, the food must be growing naturally. Grain it will not accept. Since places where suitable fodder is to be found growing are often more than thirty miles apart, this presents a considerable inconvenience to the owners.

Concerning its uses as a beast of burden, the yak itself is used both as a pack animal and for riding. According to all accounts it is an animal of rather uncertain behaviour, being liable to make attempts to cast its load, or to charge without incitement at the unwary stranger. Because of this, it is only with very great difficulty that it can be persuaded to perform tasks such as drawing the plough. For these purposes, therefore, the more docile half-bred animals, the zo and the zomo, are usually employed. These are crosses between the yak and the zebu, a type of ox used in tropical regions. The zo is the product of the cross between a male yak and a female zebu; the zomo the converse. In many ways they seem to be intermediate between their parents, and their enhanced docility as compared with that of the yak is an illustration of this. Detracting from their assets is a certain loss of size and strength, and so the purebred yak is still to be preferred for any heavy work which it can reasonably be trusted to perform.

The yak is a member of the family *Bovidae*. This family, a subdivision of the cloven-hoofed mammals (that is, Artiodactyla), also includes all cattle, sheep, goats, and animals less important economically, like antelopes and gazelles. Clearly, therefore, its importance in human history is quite immeasurable, both because of the motive power that members of the family have provided, and probably even more because of their importance as a supply of food. As with many words in popular usage, what exactly is meant by "cattle" is somewhat vague. In its narrow sense it includes only members of the genus *Bos*. This genus, as it is usually defined at present, comprises our familiar British cattle and the zebu.

The species to which our British cattle belong obviously includes many different varieties, of which those found in this country are only some. Their use in Britain at the present time, as we all know, is confined to the provision of meat, milk, and hides. Over much of the world, including many parts of Europe, however, they are still in frequent use as drawers of carts or ploughs. In Hungary, for instance, Pandolian cattle, a large lean variety, are used as draught animals, and a similar type is used in Italy. Even in Britain cattle were formerly used more for draught than for any other purpose: the horse has ousted them from this position only within the last century. In South Africa, where the great obstacle to the maintenance of domestic animals is tsetse-fly-borne disease, cattle have been particularly important. The horse, being exceptionally susceptible, was largely debarred from extensive use in that country. The ox, being much less affected, for long constituted the only means of long-distance transport in those parts, and is still the principal beast of burden there. Naturally, its importance has diminished with the development of railways, but it continues to be used in the less developed areas.

As draught animals, cattle are not so powerful as horses of comparable size. Their strong point is their capacity for travelling over rough ground, and they will continue to pull where most horses refuse to make any further effort. Regarding their behaviour from another angle, we can truthfully describe them as being, on the whole, very docile. Much of this docility is undoubtedly due to human intervention. Cattle have been associated with man for many centuries, and throughout this time their reproduction must have been subject to a certain amount of interference. Even if the better behaved animals were not deliberately encouraged to breed, those which were least tameable were no doubt generally the first to be killed for food, leaving the others to live longer and so produce more offspring. Another important point is that docility is enhanced by castration. The operation, therefore, is frequently done to bulls to be used for burden. Strictly speaking, in fact, an ox *is* a castrated bull. It has been suggested that the practice was originally performed as part of a religious ritual (in all likelihood the reason it was done to man, too), and that during this time the effects on the behaviour of the animals were regarded as incidental. Later the religious significance dwindled, and the effect of castration in promoting tractability assumed greater importance.

At first the ox was harnessed to the plough or cart simply by means of a rope tied round the horns. Later, this was elaborated by the use of a bar attached to the horns of each of a pair of oxen. Later still, a beam was rested on the shoulders of the pair, and from this thongs passed under the throat of each animal. The latter method is much the most efficient, since the horns are not always firm, and even when they are, a sudden strain is liable to snap them. The fact that oxen are always yoked in pairs is also noteworthy. This is partly because a double yoke is easier to construct than a single one, and partly because a young ox is customarily trained to its task by yoking with a fully-fledged animal.

The use of the ox as a draught animal is the usual channel along which its muscular energy is directed. Occasionally it is used in other ways, such as for riding, and as a pack animal. Its build is really not very suitable for work of this kind, however, and such practices are not very prevalent. One African tribe uses cattle in the same way as the ancients used the elephant, namely, for charging the enemy's ranks, but this again is an isolated case. A more widespread use, and one which a stretch of the imagination would allow us to consider as a further illustration of the employment of cattle in transport, is the utilisation of their skins. The skin is made airtight, inflated, and then used in the same way as a pair of water-wings. It was these tactics that enabled the Mongols to cross river after river in their assault upon Europe in the Middle Ages. The skins could alternatively be used as water bags, and every soldier in this, and in many other armies, carried one as a regular part of his equipment. Cattle were not, of course, exclusive in providing skins for these purposes, but their utilisation was very general.

Apart from the types of cattle we have been discussing, the only animal normally included in the genus *Bos* is the zebu. This is to be found mainly in India, where it is held sacred by the Brahman Hindus. Throughout the peninsular region of that country it is also the commonest beast of burden. It differs markedly from other cattle in the possession of a hump composed of fatty tissue on its back. This is a favourite dish in India, and is, incidentally, very conveniently situated for keeping the yoke in place.

We have dealt with cattle in the narrow sense. In its broader sense the term includes, not only those just mentioned, but also the bison, yak, buffalo, and a few less familiar animals, such as the banteng and the gaur. Of these, the yak has already been discussed. The buffalo we may fairly regard as one of man's most exacting experiments in domestication. The only species for which it has actually been achieved is the Asiatic water buffalo. This is a large animal, which, in its wild state, is considered to be India's most dangerous animal next to the tiger. Even when domesticated it can be trusted only with those with whom it is familiar. Strangers are frequently attacked without provocation. If we pass over these unfortunate features, however, we find many advantages. Chief among these is its strength, which, both as regards carrying and draught, is exceeded only by the elephant's. Another important point is that it will thrive in hot moist regions to which ordinary cattle are unsuited. This latter quality has resulted in its being widely employed throughout southern and eastern Asia. It has also been introduced into parts of Europe, such as Italy. Like all domesticated members of the cattle group, it serves not only as a source of power, but of meat and milk.

The American buffalo is not closely related to the one we have just been discussing, and is more properly known as the bison. Attempts to domesticate it have been made on several occasions, but none have been sufficiently successful for it to have become definitely established in such a rôle. The success with which recent experiments in this direction are said to have met, however, suggests that this was due, more to the half-heartedness of the previous attempts, than to the intractability of the animal.

Though it has no direct bearing on our present subject, it is interesting to note that the bison has been successfully crossed with breeds of ordinary domesticated cattle to produce a fertile hybrid. This has been christened the cattalo. Furthermore, it appears that this capacity for interbreeding to produce *fertile* offspring extends to the whole cattle group (taking the word in its broad sense), with the exception of the buffaloes. Yet this group is divided not only into several *species*, but into several distinct *genera*. I mention this merely because it furnishes an everyday illustration of the incorrectitude of regarding different species as being necessarily intersterile.

Of Bovidae other than those we have been discussing, only sheep and goats are domesticated. These are kept mainly for a food supply, and only very rarely used as beasts of burden. Both are occasionally used to carry small loads or to draw small carts, and in Tibet some large breeds of sheep are regularly employed for the more serious purpose of carrying loads of salt and borax. Pigs, also cloven-hoofed, but of a family different from the Bovidae, are kept for their flesh alone.

The undivided-hoofed mammals (that is, Perissodactyla) which are of importance to man are confined to the family *Equidae*. This family includes the horse, ass, mule, and zebra. At the present time the horse is probably the most widely used of all beasts of burden. Its qualities, of course, vary considerably with the breed, but it is reasonable to describe it as being, in general, an animal which combines a considerable degree of strength with a capacity for travelling unusually fast over prolonged periods. Altogether, it is much the most suitable means of animal transport wherever the country is fairly firm and even. Needless to say, there are occasional exceptions to this—the limitations imposed by the tsetse fly on its use in South Africa are an example—but speaking broadly the statement holds good. In Britain, of course, the use of the horse for riding and draught is its main one. To a lesser extent it supplies us with hair for stuffing, and skin for leather. Probably this emphasis on its utility as a beast of burden holds good the world over, though peoples such as the Kazak of Central Asia regard both the meat and milk as delicacies. Our prejudice against the former would seem a quite irrational one. Our failure to utilise the latter is more understandable, as the mare yields milk for only a fairly short period after foaling, and during this time requires several milkings per day. We may note, however, that in ancient times these disadvantages were not sufficient to prevent the milking of mares from becoming a very widespread practice.

In spite of the inferiority of its strength as compared with that of the horse, the ox long held an almost exclusive monopoly of all heavy draught work. The reason for this was no doubt largely as follows. The horse assumed importance as a domestic animal only when the use of oxen harnessed by a yoke had already become an established practice. What could be more natural, then, than to transfer the ox yoke straight to the horse? The fact that this was done without any alteration was unfortunate, for the ox yoke pulled against the horse's throat at a point where the windpipe was near the surface, and greatly reduced the efficiency of the animal. Yet in spite of this manifest defect, it was not until the ninth century A.D. that a rigid horse collar, pulling on the shoulders as a harness should, was introduced.

Notwithstanding the horse's strength, its speed was of still greater account, and throughout history its main function has been as a rapid means of transport. But in particular it has been associated with war. From ancient Egypt and Sumer we have numerous representations testifying to the use of the horse-drawn chariot in battle, and in nearly every period or place some such connection is to be found. In North America, for instance, the introduction of the horse by the Spaniards was followed by the adoption of riding by many tribes as a means, primarily of hunting bison, but also of raiding other tribes. Later, to the great benefit of the early film industry, white settlers were also attacked with its help. In Britain, again, a large horse like the Shire, now used only for draught, is descended from a large old English breed originally valued because of its ability to carry a man in full armour. It was, in fact, not until the eighteenth century that our horses came to be used for heavy work such as drawing the plough. At present, as we are all aware, there is what is really a quite remarkable specialisation into the very large and strong types used for the heaviest work, and the slender saddle horses used for riding, and drawing light carriages. Between these are the intermediate harness horses. At what stage these different types diverged from one another is a matter which has not been settled.

Admirable though the horse is in many ways, the demands it makes for its care are considerable. It must, for instance, have both food and drink at frequent intervals. In the case of the Bedouin of Arabia, a people who depend mainly on their camels, but who, paradoxically, prize horses above everything, the amount of care and attention lavished is quite extraordinary. A family will not hesitate to go short of food in order to provide sufficient for the all-important horse. Yet in spite of all this, the animal is hardly used except as an occasional means of making raids.

Partly because of its smaller size, the ass (or donkey), a near relative of the horse, cannot travel so fast, or bear quite so heavy a load as the latter. But in certain of its features—its capacity for going without water for considerable periods, and its surefootedness, for example—it is at an advantage. In this country the ass is hardly used at all, and actually our climate is not very suitable for it. It is only in hot climates that its use becomes really frequent, and under these conditions it thrives much better than the horse. Particularly in the Near East, it has been important for riding, and even more as a pack animal, from very ancient times. The surefootedness of the animal makes it especially useful in mountainous districts, and the Egyptian Expeditionary force of the 1914-18 war found it necessary to fall back on it when operations extended into hilly country. In some of the mountainous parts of

South America, too, its use for carrying baggage is fairly extensive; here it is known as the burro.

The mule, the almost invariably sterile hybrid offspring resulting from the horse-ass cross, combines some of the advantages of both its parents. It is as large as a horse, and can travel much faster than a donkey. At the same time it retains much of the latter's surefootedness, and ability to thrive on poor fodder. On top of this, its period of fitness for hard work is unusually prolonged. With rare exceptions it is used entirely as a pack animal.

These three animals—the horse, the ass, and the mule—are, relatively speaking, very docile and readily trained. This is particularly true of the horse. The ass and mule have a reputation for stubbornness, but exhibitions of behaviour of this sort are not really sufficiently frequent to interfere seriously with their utility as beasts of burden.

In South Africa, the zebra and quagga, also members of the family Equidae, have from time to time been used for drawing vehicles, and riding. South Africa is the natural home of these animals, and we should expect the immunity to tsetse-fly-borne disease which, understandably, they have developed, to make them of particular value there. According to all accounts, however, the zebra, at least, can be trained only with difficulty, and requires little incitement to bite or kick. (Actually, "zebra" is a rather arbitrary name, and includes two species quite as distinct from one another as either is from the quagga). The quagga, it appears, was rather more tameable, but since, thanks to the efforts of game hunters, it has now been extinct for over fifty years, information regarding its habits is somewhat vague.

I have, I think, mentioned almost every animal which is, or has been, of any importance as a beast of burden, and most of those which have been extensively associated with man in any way. But clearly, these are not the only ones which are at all tameable. As long as its trainer is skilful or patient enough, almost any mammal seems to respond to training at least to a sufficient degree to be safely handled. Moreover, of those which *are* extensively domesticated, some, the water buffalo and the yak for example, are not by any means conspicuous for their tractability. What, then, decides which animals are to be domesticated, and which rejected? Perhaps *physical* qualities are all-important. But obviously this is a gross over-simplification. Why, for instance, did the natives of North America never utilise the source of animal motive power they had in the caribou or the bison? Why did the natives of South Africa never exploit the elephant, the buffalo, the zebra, or any of the types of antelope so common there? The question is a complicated one, and must be considered from many points of view. And we must be clear at the outset that we are unlikely to obtain a satisfactory answer as long as we continue to seek an explanation in consciously planned *motives*.

We of the mechanised West keep animals lacking any economic value as playthings, and primitive peoples frequently do the same. There is no reason, therefore, to deny the existence of similar habits among the people of prehistoric times. This being so, many animals may originally have become associated with man in this way. It is very probably true, for instance, of the dog and the cat. For larger, and less easily fed animals, such an origin is not so likely. Another circumstance to which attention has been drawn in this connection is the proximity into which man and animals are thrown when both congregate round an oasis. The likelihood of such proximity having been important in the initiation of domestication, it is pointed out, is increased by the fact that the Middle East, the probable site of the beginnings of domestication for several animals, was subjected to a period of increasing drought at just about the time when these same animals are likely to have begun their association with man. In contrast to this situation, where we have animals remaining in the vicinity of human settlements for considerable periods, the bison of North America, to take one instance, are continually on the move. The wide extent of their seasonal migration means that there is never any likelihood of their remaining near man for any length of time. This, it has been suggested, probably accounts at least in part for the fact that the Indians never achieved the stage of tending bison in herds, rather than hunting them down in the wild state.

The points we have just considered—the effects of keeping animals as pets, and of their congregation round oases—are merely two illustrations of the sort of thing to be taken into account in any serious attempt to analyse the whys and wherefores connected with the domestication of animals. With the space at our disposal we shall, perforce, have to leave it at that. Before concluding, however, I should like to emphasise that whatever the reason for their adoption, those beasts of burden we do possess, and have possessed, have unquestionably been of immense importance in human history. Speaking generally, their most significant rôle has undoubtedly been that played in connection with transport. To catalogue all recorded instances testifying to this would be a lengthy task, but it is not necessary to do this to realise the effect that their use must have had on the diffusion of materials and ideas from one part of the world to another. Before the advent of mechanised vehicles their employment in overland travel constituted the only alternative to hiking. At least, therefore, they greatly increased the speed of communication, and made possible the carriage of much heavier loads. At most, the result of their use was to open up channels of transport through regions which had previously presented virtually impassable barriers.

FURTHER READING

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GLOSSARY

ACCOMMODATION. Changing the focus of the eye. In man this is done by altering the curvature of the lens.

ALGA. Non-flowering plant, usually aquatic, containing chlorophyll. There are several groups of algae including the green, brown and yellow-green. The green frothy scum often seen in ditches usually consists of *green algae*, and most of the common seaweeds are *brown algae*.

AMPHIPOD. A member of the order Amphipoda of the sub-phylum Crustacea. Most of them are shrimp-like animals flattened from side to side, which swim on their sides, *e.g.*, the fresh water shrimp often found in watercress.

ANTIBODY. Antibodies are an important part of the defence mechanism of a vertebrate animal against invasion by bacteria, viruses and other parasites. When bacteria or viruses or their poisonous products, or many other foreign substances, gain access to the tissues, the animal responds with the production of certain proteins, which are the antibodies. At least one specific kind of antibody is produced for each kind of foreign substance. The antibody combines chemically with the foreign substance, and in the case of virus, bacterium, or their products, makes it harmless or helps to do so. It is still uncertain where in the body antibodies are formed, but once produced they occur mainly in the blood. Immunity to disease conferred by vaccination or inoculation is due to antibodies.

AUTOCATALYTIC. Catalysing its own production. A catalyst is a substance which, in minute amounts, strongly promotes a chemical change without itself being used up in the process.

BACTERIOPHAGE. A virus which multiplies in, and destroys, bacteria.

BIOMETRICAL METHODS. Methods involving measurement of the characteristics of living things, and the application of statistical techniques to these measurements.

BRASSICA CROPS. Crops of plants belonging to the cabbage family, *e.g.*, brussels sprouts.

CARBONIFEROUS. Geological period 240 to 320 million years ago. Time of formation of the great coal deposits.

CELL. Both animals and plants are built up of microscopic units called cells, stuck together and supported by intercellular material. Cells are of very various form and function, but they all have certain characteristics in common: (*a*) They are bounded by a membrane which allows some substances to pass through, but not others. (*b*) They contain one or sometimes several nuclei (each of which contains a set of the genes, or hereditary factors, which the organism has received from its parents). (*c*) Inside them go on most of the vital processes—essentially the synthesis of new material, and the destruction of other substances which liberate energy. Every animal and plant reproduced sexually starts life as a single cell (formed by fusion of a male and a female cell). This cell divides into two, and by continuous doubling the adult's millions of cells are formed.

CENTRIFUGE. A machine which stratifies liquids, or particles suspended in liquids, according to their density. Its effect is to speed up the sedimentation due to gravity which occurs on standing. It does this by spinning the material very rapidly, and so applying centrifugal force. Under certain conditions the size of suspended particles can be estimated by the speed with which they move under a known centrifugal force.

CHITINOUS INTEGUMENT. The superficial covering or integument of insects is of firm tough material which is largely *chitin*. Chitin is chemically related to the sugars.

COELENTERATES. A phylum of animals which includes the hydroids, jelly fish, sea anemones, and corals. The hydroids are mostly small and fairly insignificant animals growing in tufts on rocks, seaweeds, etc.

COLLAGEN. Tough fibrous material which occurs in most organs of an animal and plays a very important part in holding the body together. Collagen when boiled yields glue. The collagen of skin when tanned is leather.

CONNECTIVE TISSUE. A kind of tissue which holds other tissues and organs together by virtue of the collagen it contains.

CRETACEOUS. Geological period 60 to 130 million years ago. Marks the end of the age of dinosaurs.

DIATOMS. Microscopic aquatic yellow-green algae, usually free-floating, with a delicate shell of silica. Of the greatest importance in the economy of the sea as a food for animals.

EDDYWORMS. Flat worms, mostly not more than 1 inch long, living in water. They are so called because they make eddies in the water, which can be seen with the microscope. They belong to the class Turbellaria of the phylum Platyhelminthes.

FEMUR. The "thigh" of insects; the third from the base of the series of rigid segments, separated by joints, which make up a leg. (In vertebrates the thigh bone).

FLAGELLUM (*plural* flagella). A long whip-like protoplasmic structure present in some bacteria, used for locomotion.

GENUS. See Species.

HYDROIDS. See Coelenterates.

INTERTIDAL ZONE. Region between high and low water marks.

ISOPOD. A member of the order Isopoda of the class Crustacea. Most of them are flat from above downwards, *e.g.*, wood louse, pond slater.

LEGUMINOUS. Belonging to the family Leguminosae of flowering plants. Includes peas, beans, vetches, etc. Characterised by the possession of nodules of nitrogen-fixing bacteria on the roots.

LEY. Temporary grass land; arable land which has been sown with grass seed and will be ploughed up again after a varying time.

MAMMAL. A vertebrate animal belonging to the group Mammalia characterised by fur (or hair), warm-bloodedness, and by the fact that their young develop at first within the mother and after birth are fed on milk. *E.g.*, dog, elephant, whale, man.

MICROTOME. A machine for cutting very thin slices of soft tissues.

MUSCLE FIBRE. The cellular unit of muscle tissue. It alters its shape when stimulated, and the co-ordinated changes in shape of numerous muscle fibres produce muscular contraction.

MUTATION. A change in hereditary constitution.

Niche. The way an animal gets its living (its "trade") particularly as regards its food.

Nitrogen-fixing Bacteria. Certain soil bacteria, some of which live in *nodules* in the roots of leguminous plants, can use the nitrogen of the air for the formation of nitrogenous substances and ultimately proteins. This is *nitrogen-fixation.* All other plants and animals are dependent on preformed nitrogen compounds.

Olfactory. Concerned with the sense of smell.

Orthoptera. An order of insects which includes the cockroachs and locusts.

Phalangid. Harvest man. Animal related to spiders, with globular body and eight very long legs, often found on walls in damp sheds.

Polyzoa. The sea mats and sea firs. A phylum of small animals which live in colonies, superficially resembling the hydroid coelenterates.

Pronotum. The plate of chitinous integument on the back of an insect just behind the head, belonging to the segment which carries the first pair of legs.

Pseudoscorpion. Animal found under rotten wood, stone, etc., related to spiders and scorpions. Sometimes called book scorpion because it may be found in libraries.

Sea-squirts (Ascidians). A class of animals distantly related to the vertebrate stock. Most are sedentary. So called from the habit of some of the larger members of contracting violently and squirting out sea water from their bodies.

Sedentary Animals—those which are fixed during most of their life, *e.g.*, barnacles. Such animals are aquatic. Their larvae are free-swimming and often very different from the adults.

Silage. Preserved plant material used for feeding to farm animals. Silage is made by allowing grass, etc., to ferment in the absence of air, and the acid formed during the process prevents other kinds of decay (see p. 44).

SPECIES. Group of all animals or plants of the same kind, *e.g.*, all domestic horses form one species. Similar species are grouped together into a *genus*. Similar genera are also grouped together, and so on in a hierarchy. Each species is known by a double scientific name, the first defining its genus, the second its species, *e.g.*, *Haemonchus contortus*.

SPRINGTAIL. Small wingless insect, so called because it jumps by sharply extending the abdominal appendages.

SUB-LITTORAL ZONE. Region of sea below low water mark, extending roughly as far out from the shore as the edge of the continental shelf (equivalent to a depth of sea of about 600 feet).

SUCCESSION. A sequence of communities of plants and animals, occupying one after another the same area. The area slowly alters in such a way that the existing community is unable to go on living there and a new community then takes its place. The alteration takes place at least partly under the influence of the existing community itself.

TAXONOMY. The science of the classification of animals and plants.

TERTIARY. Geological period 1 to 60 million years ago. The age of mammals. End of this period is marked by the ice ages which occupied the last million years.

ULTRA-FILTRATION. Filtering through very fine pores. If a series of filters of known pore-size is used, the size of particles which just fail to pass a certain filter can be obtained.

VACCINIA. Cowpox, a virus-caused disease very closely related to smallpox. The virus of vaccinia produces antibodies which act on the virus of smallpox. Artificial immunity to the latter is therefore produced by vaccination with Vaccinia virus.

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